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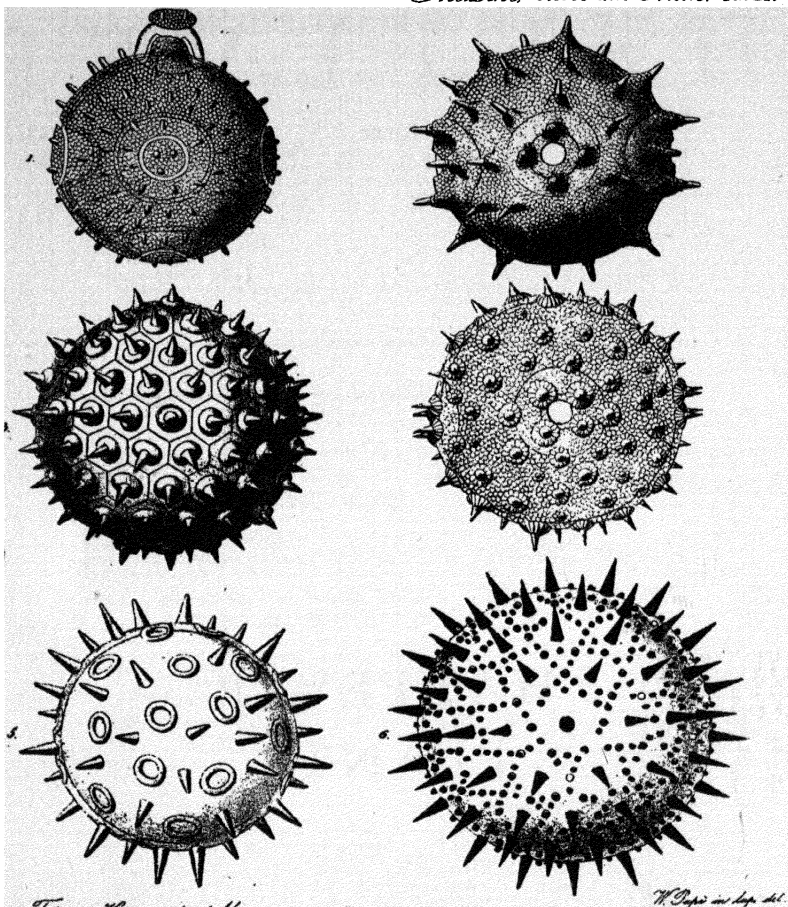
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- 1935 — POLLEN GRAINS
(*The McGraw-Hill Co., New York and London*)
- 1936 — EVOLUTION OF POLLEN GRAINS
(*Botanical Review*, vol. 2)
- 1939 — WEEDS, WASTE AND HAYFEVER
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Volume XV

HAYFEVER PLANTS



The six illustrations of pollen grains here reproduced are from one of the beautiful hand-colored lithographic plates of KARL JULIUS FRITZSCHE's immortal work, *Ueber den Pollen*, published at St. Petersburg in 1837.

Figure one shows the grain of the common squash or field pumpkin (*Cucurbita Pepo*). The grain has absorbed moisture causing the protrusion of its contents as a papilla through one of its germ pores. Figure two shows a side view of a grain of "*Astrapaea penduliflora*," a member of the genus generally called in modern texts *Assonia* of the Sterculiaceae, and to which the Zulu cherry belongs. Figure three is of a grain of "*Sida abutilon*" of the Malvaceae. In the original plate it is colored a deep yellow due to its superficial coating of yellowish oil. Figure four is of the same grain as it appears when immersed in water and oriented so as to bring one of its germ pores uppermost. Figure five shows a sterile grain of the Chinese hibiscus (*Hibiscus rosa-sinensis*). It is nearly colorless and transparent because, being sterile, it is quite empty. Figure six shows a grain of the common hollyhock ("*Alcea rosea*"). In the original plate this grain is shown a bright pink color with the spines a deep red. This is because it was treated with strong sulphuric acid which dissolves out the cell contents and changes the color at the exine from yellow to bright red. These two latter species belong to the Malvaceae as does *Sida abutilon* of which the pollen grain is shown in figures three and four.

Though the work of FRITZSCHE was done more than a hundred years ago, his splendid plates have been seldom equalled in beauty, clarity and truthfulness.

HAY FEVER PLANTS

*Their Appearance, Distribution, Time of
Flowering, and their Role in Hayfever,
with special Reference to North America*

BY

ROGER P. WODEHOUSE, Ph.D.

*Associate Director of Research in Allergy, Lederle Laboratories,
Pearl River, N. Y.*



1945

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P R E F A C E

The study of hayfever falls into two fields — the clinical and the botanical — each so broad of scope and widely differing in character that for one to excel in one is almost to preclude the possibility of excelling in the other. The past twenty-five years — approximately the time since pollen has been generally recognized as the cause of hayfever — has seen the accomplishment of much excellent work in both fields, but that of the former greatly exceeds that of the latter, and the facts of the latter field still remain scattered and so mingled with fancies that one who is not a trained botanist could scarcely be expected to separate them. This book is intended, therefore, to interpret the botanical facts of hayfever in terms of their clinical significance.

Here are described all of the plants known to cause hayfever, most of those reasonably suspected of doing so, and many which have been mentioned in hayfever literature, possibly wrongly. In the plant descriptions I have not attempted to define the species beyond pointing out a few of the salient features which may readily be used and most easily retained in memory.

The plants are presented in the sequence of ENGLER and PRANTL in their "Natürliche Pflanzenfamilien". In the choice of botanical names usage and expediency have been my guides. Nor have I attempted to settle the questions of priority, nor even to make the names conform either to the "International Rules of Botanical Nomenclature", or to the "American Code of Botanical Nomenclature". For the names of the grasses I have followed principally HITCHCOCK; for those of trees principally SARGENT; for those of cultivated plants BAILEY; and for those of the ragweeds and their relatives RYDBERG. Otherwise I have given primary choice to names of current usage especially in hayfever literature, except where these have appeared to be definitely wrong or misleading. Where more than one name is commonly used those of secondary choice are added as synonyms.

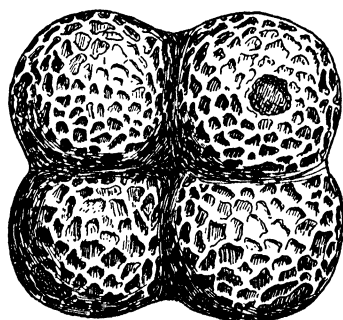
*For the capitalization of specific names, since these are all Latin or at least Latinized in form, it seems that one has no choice but to follow the Latin rules for capitalization. Consequently names of people and names of genera which are used as nouns, are always capitalized, while names of countries and places which are used as adjectives are not. Hence the capitalization in such names as *Populus Sargentii*, *Cynodon Dactylon*, but lack of capitalization in such as *Artemisia canadensis*. English names are given as far as these are known to the*

author. In fact an attempt has been made to present all the vernacular names which have any use or value whatever, but some which are obvious translations of the Latin or otherwise useless have been rejected. Where more than one vernacular name is given, the name of preference is placed first.

All of the illustrations are the work of the author, except where otherwise indicated. Those of plants were prepared from living or occasionally herbarium specimens especially for this volume.

It is a pleasure to acknowledge my indebtedness and express sincerest appreciation of the generous help I have received from friends and colleagues. Especially am I indebted to Professor L. R. ABRAMS for reading the sections on the regional botany of the Southwest, and of southern California, and to Dr. JOHN H. BARNHART for help in solving questions of nomenclature, and to Professor W. F. WELLS for the description and figure of the Wells Air Centrifuge, to Dr. RALPH BOWEN for reading the manuscript, and to Professor G. ERDTMAN for the description and figure of the Aerosol Collector. I am also indebted to the director and staff of the New York Botanical Garden, where much of the work was done, for the use of the herbarium and library and much incidental assistance.

THE AUTHOR



To win the secrets of a weed's plain heart.—
JAMES RUSSELL LOWELL (*Sonnet XXV*).

The thorns which I have reap'd are of the tree
I planted; they have torn me, and I bleed.
I should have known what fruit
would spring from such a seed.—

LORD BYRON.

Upon the land of my people shall come up thorns and briers;
yea upon all the houses of joy in the joyous city.
ISAIAH 32:13.

Cursed is the ground for thy sake; in toil shalt thou eat of it all the days
of thy life;
Thorns also and thistles shall it bring forth to thee; and thou shalt eat the
herb of the field.

Genesis 3: 17, 18.

Grass is the forgiveness of nature—her constant benediction. Fields trampled with battle, saturated with blood, torn with the ruts of cannon, grow green again with grass, and carnage is forgotten. Streets abandoned by traffic become grass-grown like rural lanes, and are obliterated. Forests decay, harvests perish, flowers vanish, but grass is immortal. Sown by the winds, propagated by the subtle horticulture of the elements, which are its ministers and servants, it softens the rude outline of the world. Its tenacious fibres hold the earth in its place, and prevent its soluble components from washing into the wasting sea. It invades the solitude of deserts, climbs the inaccessible slopes and forbidding pinnacles of mountains, modifies climates, and determines the history, character, and destiny of nations. Unobtrusive and patient, it has immortal vigor and aggression. Banished from the thoroughfare and the field, it abides its time to return, and when vigilance is relaxed, or the dynasty has perished, it silently resumes the throne from which it has been expelled, but which it never abdicates. It yields no fruit in earth or air, and yet should its harvest fail for a single year, famine would depopulate the world.

JOHN JAMES INGALLS (*Blue Grass*).

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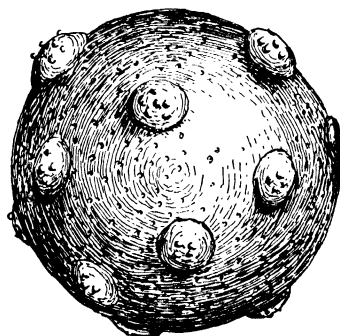
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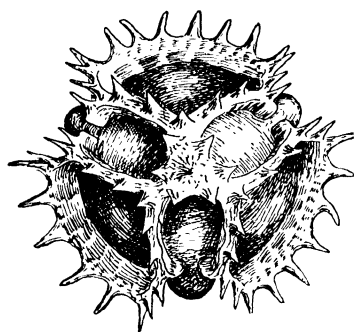
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Chapter I

THE BOTANY OF HAYFEVER

The Flower: — The purpose for which all flowers are designed is that of securing transportation of their pollen from the flower or one plant to that of another of the same species. The two principal agencies by which this is accomplished are insects and wind. A few aquatic plants, like eel grass, are pollinated under water; a few, like tape grass (*Vallisneria*) and water grass (*Elodea*) are pollinated on the surface of the water; and a few are pollinated by humming birds, snails and other agencies. But the majority, certainly all those which concern us in hayfever studies, are pollinated either by insects or by wind or by both.

In spite of the enormous variety of form of flowers they are all built on the same general plan. The same elements of construction are used in the

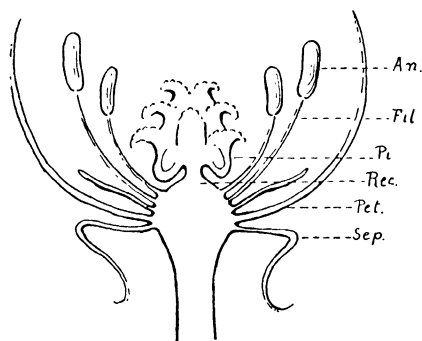


FIG. 1. — Buttercup (*Ranunculus acris*) flower, longitudinal section, diagrammatic to show the parts of a flower: — An., Anther; Fil., Filament; Pi., Pistil; Rec., Receptacle; Pet., Petal; Sep., Sepal.

different forms in varying size, shape, color and arrangement, a circumstance which makes their understanding easy when once the plan is learned. The common buttercup (fig. 1) offers an example of a flower of which the elements of construction are relatively simple, representing a form from which the others may have been derived. If the flower is split in two vertically it will be seen that the top of the stem is carried well up into the flower ending in a dome-shaped expansion, the *receptacle*, upon which the parts of the flower are assembled. These are arranged in four series known as the *calyx*, *corolla*, *stamens* and *pistils*. The calyx or outer series consists of generally five greenish or colorless parts called individually *sepals*. These enclose the more vital parts in the bud, protecting them from injury until it opens. After which they are likely to fall away. So, unless the flower is observed in the bud or very young, the sepals may be missing. Within the

calyx is found the *corolla*, consisting of the same number of parts as the calyx, generally five, which are called the *petals*. These are golden yellow in the buttercup and each is supplied with a nectariferous pit and scale at the base of the blade. The calyx and corolla together are called the *perianth* because they are arranged around the flower. Inside of the corolla are the *stamens*, variable in number. Each consists of a short stalk, the *filament*, curving upward and outward and bearing at its tip a two-lobed sac, the *anther*, in which the pollen is borne. Each lobe of the anther bears a longitudinal groove along which it may split open in due time, and if the flower is about to shed its pollen a moderately strong lens will reveal the grains starting out from the clefts. Above the stamens the receptacle is abruptly narrowed and extended upward to a point bearing the *pistils*, in this case also called the *carpels*, each consisting of a swollen base known as the *ovary* since it contains the ovule, and a short outwardly curving projection known as the *style* of which the upper side, which is called the *stigma*, is sticky and specially designed to catch the pollen grains and provide them with the proper conditions of moisture and nutriment to stimulate their germination and sustain their growth.

The essential parts of the flower are the stamens and pistils, for they alone produce the pollen and ovules which perform the necessary functions of the flower. In some plants either the calyx or corolla, or both, may be absent but still the flower is regarded as perfect. In others some of the flowers have only stamens and some only pistils. Such flowers are imperfect, and if the staminate and pistillate flowers are both on the same plant, they are called *monoecious*, and if on different plants, *dioecious*. Flowers with such extreme modifications are common among hayfever plants. For example, the ragweeds and cockleburs are monoecious, with the staminate flowers arranged in spikes at the ends of the branches and the pistillate just below.

Entomophilous Flowers: — Insect pollinated or entomophilous flowers generally have some obvious method of attracting insects, by scent which may be either pleasant or unpleasant to our senses, or by bright and conspicuous colors, which are generally exhibited by the corolla as in the buttercup and lily, by the calyx as in the hepatica and anemone, by the stamens as in *Callistemon* and *Acacia*, by transformed leaf bracts as in the dogwood (fig. 2) and poinsettia, or by the whole inflorescence as in the cockscomb and globe amaranth. They generally produce nectar which serves to encourage the visits of insects, though many flowers are visited solely for their edible pollen, and others, taking advantage of the insects' gullibility and uncontrolled sex reflexes, are merely a snare and delusion, offering the insect nothing for his visit; some of the orchids are like this. The stamens of entomophilous flowers are generally protected by the floral parts so that the pollen can not be easily reached except by an appropriate insect, and the pollen is usually sticky and not easily blown away by the wind. In general the more perfect the adaptation to insect pollination the smaller the amount of pollen produced, for the flower is primarily a device for securing pollination with the minimum expenditure of pollen.

By this criterion the orchids rank highest among the flowering plants. Their pollen is produced in masses, the grains united in fours and these in turn bound tightly together by webby filaments. The pollen masses are often provided with a sticky disk by which they become cemented to the head or proboscis of a visiting insect. They become so firmly attached to the body of the insect that he is often quite unable to detach them, except by visiting another flower when they stick to the stigma. Such pollen can not possibly cause hayfever.



FIG. 2. — Dogwood (*Cornus florida*) flowers, an example of entomophily with showy bracts.

Another example of highly perfected insect pollination is found in the milkweeds (fig. 3). Here again the pollen grains are all united into compact masses and so fixed in the anthers that they can not be removed except by an excited insect letting his foot slip into one of the tiny clefts of the flower, when the pollen mass clamps firmly onto his foot and can only be removed by bringing the pollen mass in contact with the stigma of the next flower he visits. Such pollen is totally incapable of causing hayfever.

In the sweet peas, clovers, vetches and related plants the stamens are tightly enclosed in the lower petal so that it is only when visited by an insect heavy enough to pull the petal down that the pollen is exposed; then it sticks to the insect's thorax and is carried away. Sometimes the pollen is

hidden in the tube of the corolla where it can not be removed except by an insect probing into the flower in search of nectar. All such highly specialized flowers can be totally disregarded as causes of hayfever. Their pollen is so closely guarded that it can not escape.

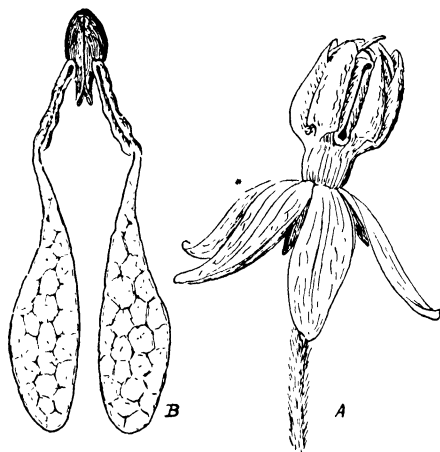


FIG. 3. — Milkweed (*Asclepias Cornuti*), an example of a flower highly specialized in entomophily; A, a single flower; B, pollinia greatly enlarged.

Imperfectly Entomophilous Flowers: — But entomophilous flowers are not always so perfectly adapted to pollination by insects. For example some kinds of goldenrod, sunflowers and dahlias are rather loose with their pollen. Often it may be found scattered on the leaves of the plants, or, if the plants are put in water in the house, it becomes scattered on the table where they are standing. If the bees do not carry off this pollen it may easily be blown away and become to some degree atmospheric. At any rate the pollen of sunflower and goldenrod is often caught on atmospheric pollen slides, though always in very much smaller quantities than that of the rag-weeds and grasses. Consequently such imperfectly insect-pollinated plants as the sunflower, goldenrod and dahlia must be given some consideration in hayfever studies. But they should not be taken too seriously.

Amphiphilous Flowers: — Still other plants are both wind and insect pollinated. An outstanding example of this class is the willow (fig. 28). Its flowers are bright yellow in color, sweet scented and abundantly supplied with nectar which is greedily sought by bees in the early spring when other flowers are scarce. By these tokens it must be regarded as insect pollinated. But if we examine the flowers closely they are found to be extremely simple. They are aggregated in spikes or catkins with the sexes entirely separate. The male flower is without calyx or corolla, consisting of just two stamens,

each in the axil of its bract with a glandular scale at its base. They produce a large amount of pollen which is only slightly sticky and floats away in the air when not carried off by insects, and may even at times cause hayfever, so by these tokens willow flowers are wind pollinated. If one method fails them they can fall back on the other.

Anemophilous Flowers:—Pollination by wind is the most ancient and primitive method. It is scarcely different from the anemophilous dissemination of spores by the ferns and fungi. It appears to have been the only method employed by the ancient gymnosperms, the *Cycadofilicales*, *Bennettitales* and *Cordaitales*, mighty races of trees of past geological ages. It is likewise the method of pollination among the living gymnosperms, such as the conifers. In fact the pines, firs, hemlocks and spruces are the greatest living practitioners of anemophily, if the amount of pollen produced is to be taken as the criterion. So much pollen is given off by these that it is sometimes to be seen floating like a cloud above the forests. It accumulates on the surfaces of lakes and ponds in such quantities that it may be scooped up by the pound. Sometimes it is washed out of the forest by heavy rains and spread over the ground giving rise to the so-called "sulphur showers".

Among the flowering plants (angiosperms) anemophilous flowers are also characterized by simplicity of structure, but this is a simplicity of reduction and not of primitiveness. They are not showy, do not produce nectar, are not scented and are of little or no interest to insects. They may produce enormously more pollen than their insect pollinated relatives—though they do not always—and this is dry and powdery. There is a marked tendency toward the separation of sexes, and for the flowers to appear early in spring, particularly among trees and shrubs, before the leaves are fully developed.

One of the most interesting things about anemophily is that it occurs in many families which are entirely unrelated, showing that it is a recent evolutionary development. It is found in the grass family; all of these are wind pollinated, except a few like the cultivated oat and some varieties of wheat, which are self-pollinated. It also characterizes all of the goosefoot family, most of the pigweed family, the plantains, and a few genera like the docks in the buckwheat family, the ragweeds and mugworts in the composite family, and many others.

What Makes Some Plants Cause Hayfever?—In order to cause hayfever pollen must have certain characteristics which may be summed up as buoyancy, abundance and allergenic toxicity. To judge if a plant is likely to cause hayfever one must discover by observation or experiment its mode of pollination. If it is entirely entomophilous it should be unconditionally excluded. There is no use in considering such plants as orchids, snapdragons, milkweeds, lupins and the many showy garden and wild flowers which are often suspected by the uninitiated. If the plant is loosely entomophilous or amphiphilous it may be suspected, especially if it belongs to one of the hayfever-plant families. Goldenrod, sunflower, chrysanthemum and stevia, for instance, belong to the composite family, the same family as the ragweeds, and they can on occasion cause hayfever. Privet and olive

belong in the same family as the ashes, and both occasionally cause hayfever. But it is only among the truly anemophilous plants that one need look for the really important causes of hayfever. And by no means all of these are important for anemophily only conditions one of the necessary attributes, that of buoyant pollen. It is frequently stated that wind pollinated plants are characterized by their production of excessive quantities of pollen. This is true of only relatively few; indeed the work of POHL (1937) shows that there is really no relation between the mode of pollination and the amount of pollen produced. Most anemophilous plants shed far too little pollen, or else the plants themselves are too scarce, to be of any consequence in hayfever. There are about 1100 species of grass growing naturally in the United States, for example, most of them wind pollinated, yet 35 would be a generous estimate of those which have anything to do with hayfever, and those which are its important causes number about seven. The others either shed too little pollen or are themselves not abundant enough.

Hayfever Toxicity: — Equally important is the allergenic toxicity of the pollen. The only way to settle with certainty the question of this is by actual clinical test with pollen-sensitive individuals. Fortunately, however, allergenic toxicity is found to be rather strictly a family character, limited to relatively few families. The most important of these are:

WEEDS AND GRASSES

Gramineae, the grasses.

Compositae, ragweeds, mugworts, goldenrods, etc.

Chenopodiaceae, Russian thistle, saltbushes and chenopods.

Amaranthaceae, pigweeds and waterhemp.

Plantaginaceae, plantain.

Polygonaceae, dock and rhubarb.

TREES AND SHRUBS

Betulaceae, birches, alder and hazel.

Fagaceae, beeches, oaks and chestnut.

Ulmaceae, elms and hackberry.

Moraceae, mulberries and paper mulberry.

Juglandaceae, walnuts and hickories.

Salicaceae, poplars and willows.

Aceraceae, maples.

Oleaceae, ashes, olive and privet.

The pollen of the grass family possesses hayfever toxicity to rather high degree, and so universally throughout the family that some authorities maintain that the pollen of one grass—generally they use timothy—is sufficient to treat sensitization to all grasses. The pollen of the composite family possesses allergenic toxicity to an even higher degree, and it appears to be universal in the family so that the relative importance of the various species in hayfever is almost entirely a matter of the buoyancy and abundance of their pollen in the air.

Other families which possess this kind of toxicity are the *Chenopodiaceae*, with Russian thistle and the saltbushes as examples, the *Amaranthaceae* with the pigweeds and water hems, the *Plantaginaceae* with English plantain apparently the only species which can qualify on other counts, and

the *Polygonaceae* possess it to only a slight degree as exemplified by the docks. On the other hand hayfever toxicity is largely lacking in other families which would otherwise qualify as hayfever plants. For example the cattails, the rushes and sedges are nearly or quite harmless in hayfever though the plants may be abundant and are often extravagant producers of buoyant pollen. Among the conifers which are mostly prolific shedders of buoyant pollen, only the junipers and their closest relatives, members of the Cypress tribe, have been shown to possess allergenic toxicity in sufficient degree to cause hayfever. It is probable, however, that in the phylogenetic classification of the conifers if the same principles of classification had been followed as is used among the angiosperms the tribe of the junipers and their allies would have been given the rank of a separate family. At any rate, admitting this exception, hayfever toxicity appears to be a family character. Generally speaking, from a hayfever standpoint, first consideration should be given to those plants which belong to families in which occur known causes of hayfever.

Regional Surveys: — In every region where hayfever occurs it is essential to the physician to know which plants are producing the pollen and exactly when each flowers and how much of each of the different kinds of pollen there is in the air.

There are three sources from which this information is obtained, field, laboratory and clinical. They are supplementary to each other in such a way that a complete picture of the pollen situation can only be gained by a combination of all three. For the field study the area in question is divided into sections. Or representative sections are chosen of convenient size. These are visited at frequent intervals throughout the hayfever season. All anemophilous plants, and others which by unusual abundance or other characteristics should be suspected, are counted, their time of flowering noted, the relative amounts of pollen shed by each determined and samples of it collected. Methods of collecting and preserving pollen have been repeatedly described (KELLY 1928, WODEHOUSE 1935) so need not be dwelt on here. Suffice it to say that almost any flowers which are capable of causing hayfever will shed their pollen if cut and placed in water. If any plants are encountered which can not be identified with certainty, specimens should be dried and sent to a local botanist or to one of the large herbaria. Botanists are usually glad to make identifications providing complete specimens are sent. Small herbaceous species should include root, stem, leaves, flowers and, if possible, fruit. Trees and shrubs should include twigs, flowers and leaves, and a note regarding the missing parts, such as "tall tree with dark grooved bark", or "spreading shrub with light gray bark". And always the date, exact locality of collection and name of the collector should accompany each specimen. In case the plant is monoecious or dioecious both staminate and pistillate flowers should be included. Most botanists feel themselves more than compensated for making the identification if given a complete and properly dried specimen with the necessary record for their herbarium (*see p. 15*).

Atmospheric Pollen: — While the field observations are being carried on atmospheric pollen counts should be made every day to discover which kinds of pollen are in the air, and their abundance. This is the laboratory part of the problem. There are several methods of obtaining pollen counts, but the one generally employed is that of simply exposing microscope slides coated with some adhesive, the adhesive used depending upon the circumstances. Unless the season is rainy or the atmosphere extremely damp, glycerine jelly is the adhesive of choice.

In order to prepare the slides ordinary commercial glycerine jelly to which a small amount of a dye such as basic fuchsin has been added, is melted on a water bath, kept at a temperature below boiling point. The slide to be coated is warmed, clamped to the revolving disk of a slide turntable and spun as in ringing slide mounts. A small camel-hair brush is dipped into the melted jelly and stroked slowly from the center of the spinning slide outward to the ring marked on the turntable which corresponds to the size of the cover glass to be used in finishing the preparation. The whole process

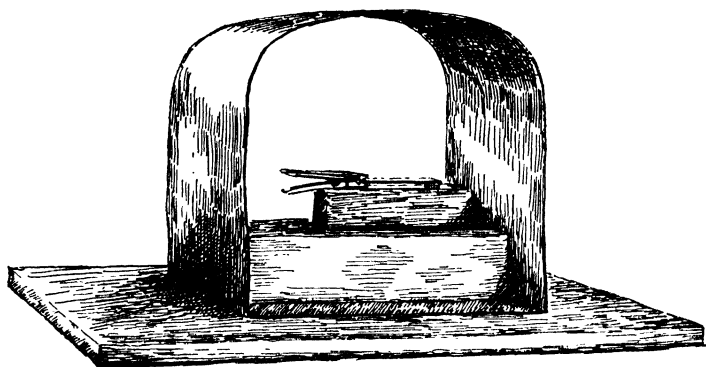


FIG. 4. — Pollen shelter for exposing atmospheric pollen slides.

takes only a few seconds, and enough slides to last a month can be made up at one time. Great care must be taken not to expose the slides to any dust during their preparation and storage lest they should become contaminated with extraneous pollen before they are used.

For exposure the slide must be fastened securely, placed in an exposed situation and protected from rain. Various kinds of shelter have been devised for this purpose. That used by the author is shown in fig. 4. It consists of a copper can about $10 \times 10 \times 14$ in. lying on its side. The top and bottom have been removed and inside the can, on its lower side, is fastened a heavy block of wood. To this is attached a smaller block to which is fastened a spring clothespin to hold the slide by one end, and a piece of cork upon which the free end of the slide may rest. The whole apparatus is nailed to a stout board which may be weighted or fastened to the roof of the laboratory or other support.

After the slide has been exposed for 24 hours it is brought in, grains of sand or other materials which might prevent the cover from settling into

place, are removed. The slide is then heated gently and a No. 0 cover glass put over and lightly pressed into place.

Vaseline Method: — In case the atmosphere is moist or showers are frequent and likely to spoil the gelatine coating of the slide, vaseline may be substituted for the jelly. To do this a small spot in the center of the slide is smeared very lightly with clean vaseline. After the slide has been exposed as above and any extraneous material, if present, removed, a small fraction of a drop of melted stained glycerine jelly or lactophenol* is added and the cover pressed firmly into place.

An interesting modification of this method is that used by REMPE (1937) in his remarkable studies on the dispersal of pollen by means of air currents. He used small brass tubes, 14 × 45 mm, with their ends wrapped with cellophane which was coated with vaseline. These he exposed by hanging in the crowns of trees or from the tops of tall poles. After exposure the cellophane was removed and pressed face down on a microscope slide for observation.

Open Dish Method: — A method described by LÜDI and VARESCHI (1936) is to expose without cover or protection of any kind a shallow dish such as a petri dish but deep enough to avoid being overflowed by rain. The bottom of the dish is covered with a thin layer of glycerine and water. After exposure the pollen, glycerine and accumulated rain water are washed out with pure water and centrifuged so as to concentrate all solid material into one or two cubic centimeters of liquid. Then this is boiled in 10 per cent potassium hydrate for three to five minutes to remove the cell contents of the pollen grains. The material may then be suspended in a measured volume of water and the pollen grains of a known fraction counted. From this may be calculated the number of grains falling into the dish per unit area.

Erdtman Air Filtration Method: — Professor G. ERDTMAN of the University of Stockholm has devised a method for filtering pollen and spores out of the air and at the same time metering the air. The apparatus (fig. 5), which he calls the Aerosol Collector, is a small vacuum cleaner with its filter bag replaced by a plaited filter paper supported on an aluminum frame. All the air which enters is forced through the filter paper, and as it leaves the apparatus is led through a pipe where it is metered. Through one side of the exhaust pipe is inserted a pitot tube, a small tube with a short right-angled bend turned so that its orifice faces against the flow of air. The pressure exerted in the pitot tube by the flowing air is transmitted by a small rubber tube to a mercury manometer. The manometer is calibrated with the assistance of an ordinary air meter so that the pressure is read in terms of cubic meters of air flowing per hour. If the manometer is read at the start and finish of a run the total amount of air that passed through the apparatus can easily be calculated. At the end of

* Phenol, 2 cc. Lactic acid, 2 cc. Glycerine, 4 cc. Water, 2 cc. (LEE, A. B. 1921).

the run the filter paper is removed from the apparatus and taken to the laboratory for analysis.

The paper with its collected spores and pollen grains is treated with acetic anhydride and sulphuric acid, 9:1, heating to boiling on a water bath, to dissolve the filter paper and other unwanted organic material. The mixture is then centrifuged, the sediment washed to free it of the reagents, and suspended in a measured volume of water. A sample of this is removed by a pipette and placed in a specially devised counting chamber (ERDTMAN 1935) similar to that used for counting bacteria but modified to adapt it to the much larger pollen grains. The counting chamber enables one to learn the number of grains of each species of pollen per cubic centimeter of the

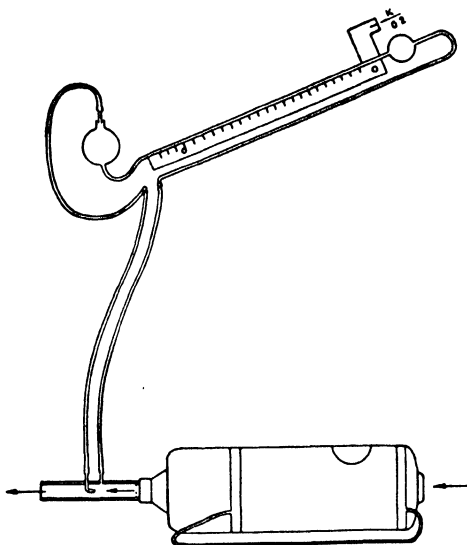


FIG. 5. — Aerosol collector, after G. ERDTMAN.

pollen suspension. From this can readily be calculated the number of grains per cubic meter of air which passed through the Aerosol Collector during the run.

The Wells Air Centrifuge*: — The Wells Air Centrifuge for Direct Microscopic Examination of Air (fig. 6) consists essentially of two concave discs face to face and spaced apart at their edges by the thickness of a cover glass. Through this marginal slit at the edge of the lens-shaped cavity, air is projected by the rapid whirling of the disc directly onto a celluloid foil which is supported in a metal collar surrounding the slit. The head formed by these two discs revolves at about 15,000 revolutions per minute, and the air is drawn into the concavity through an opening at the center of the

* Contributed by WM. FIRTH WELLS, University of Pennsylvania.

upper disc and thrown out through the annular slit at the rate of about 3 cubic feet per minute. The impinging velocity resulting from the enormous centrifugal force developed causes particles within the air to be deposited upon the film in a ridge at the angle where the air changes its direction sharply toward the outflow.

The lower of the discs is attached by a flexible rubber sleeve to the shaft of the motor, and the upper to the collar in which the celluloid is placed and from which it can readily be removed. The insertion and removal of the celluloid strip is thus facilitated, after which it can be cut and fixed to a glass slide for direct examination, or otherwise manipulated if further treatment of the deposit is desired.

Sampling then reduces to insertion of the celluloid strip and spinning the centrifuge for a period depending upon the volume of air it is desired to sample. A cubic meter of air is sampled in approximately ten minutes.

Counting is simplified if the ridge of deposit is mounted parallel to the edge of the slide or is in the direction of motion of a mechanical stage. A low power objective is brought over the densest part of the ridge at one

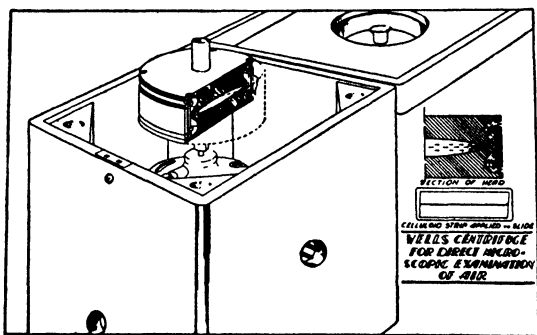


FIG. 6. — Wells air centrifuge, after W. F. WELLS.

end and the slide is made to traverse the length of the ridge under the eye of the person counting. One additional traverse above and one below the central traverse should include most of the particles, but if more than 10 per cent of the count of the central traverse is obtained in either lateral traverse, another traverse should be made further from the center.

The entire machine is contained in a small portable box, the complete weight of which is about ten pounds. The model illustrated is equipped with a universal motor, but it is possible to replace it with one running on storage battery current. The essential part of the machine being the specially designed head, other adaptations may be devised if only provision is made for rapid revolution of the head with access to the air to be sampled.

Film, obtained from the Celluloid Company, Newark, New Jersey, and cut into $\frac{3}{4}$ -inch strips with an ordinary photographic trimmer has been entirely satisfactory.

Gravity Methods:—None of the gravity methods gives a reliable index to the absolute amount of pollen in the air, though it seems that they could be correlated with the Erdtman filtration or some other absolutely volumetric method. However, the number of grains per unit area falling on the slide or surface of liquid can be assumed to depend upon two factors, the abundance of the pollen grains in the air and their rate of fall. Upon this basis SCHEPPEGRELL (1922) has worked out a formula which was supposed to show the relation between the number of grains falling on a unit area in a given time and the number suspended per unit volume of air which is:

$$n = \frac{7 \times N}{v \times t}$$

where n equals the number of grains per cubic yard, N the total number falling on one square centimeter, t the number of hours exposure, and v the velocity of fall in feet per second. The velocity of fall (v) SCHEPPEGRELL stated he calculated from the formula,

$$v = \frac{2g r^2}{9k} \text{ (Stoke's law),}$$

where v equals the velocity of fall in cm per second, g the acceleration of gravity, r the radius of a falling sphere, and k the coefficient of viscosity of air. The velocities of fall thus calculated for pollen grains of all sizes he furnished in a table. Even if SCHEPPEGRELL had made his calculations correctly it is doubtful if they would have more than theoretical interest for they take no account of the shapes of the grains, which in their dry condition are hardly ever spherical, nor of their sculpturing. Nor do they take account of such variables as the specific gravity of the grains, the temperature and humidity of the air, and the velocity of the wind and direction in which it impinges on the slide—slides placed vertically in the air current often catch more pollen than those placed horizontally. However, much more serious than these omissions was an unfortunate error which SCHEPPEGRELL made in applying the formula of Stoke's law. In making his calculations he used the measurements of the *diameters* of the pollen grains instead of their *radii*. Since these are squared his mistake introduced a relatively huge error, rendering all of his table useless. This error of SCHEPPEGRELL's has had a far-reaching and damaging effect on succeeding investigations, for it became the custom of some of the most productive investigators in the study of atmospheric pollen to report their results in terms of pollen grains per cubic yard, accepting without question SCHEPPEGRELL's formulae so that their records are more misleading than useful.

Attention was first drawn to SCHEPPEGRELL's error by COCKE (1937). Applying the correction, he furnished a table, which he recommends to be accepted as standard form, part of which is as follows:

Velocities of fall and formulae for computing concentration per cubic yard from the number (N) of smooth pollen per square centimeter on slides exposed for 24 hours: —

DIAMETER IN MICRONS	VELOCITY OF FALL, FT. SECOND	FORMULAE
10	0.01	n = 29.1 N
12	0.014	n = 20.8 N
14	0.02	n = 16.6 N
16	0.026	n = 11.2 N
18	0.03	n = 9.7 N
20	0.04	n = 7.3 N
22	0.049	n = 5.9 N
24	0.058	n = 5.0 N
26	0.068	n = 4.3 N
28	0.079	n = 3.7 N
30	0.09	n = 3.2 N
32	0.10	n = 2.9 N
34	0.11	n = 2.7 N
36	0.13	n = 2.2 N
38	0.15	n = 1.9 N
40	0.16	n = 1.8 N

Reproduced from COCKE (1937).

In discussing the importance of applying the correction COCKE points out that FEINBERG and STEINBERG (1933), in correlating their pollen counts with hayfever symptoms by applying SCHEPPEGRELL'S formula, found that their pollen counts indicated that 25 grains of ragweed pollen per cubic yard was sufficient to produce symptoms, or 500 inhaled per day. Whereas, correcting for SCHEPPEGRELL'S error and allowing for the spicules on the ragweed pollen grains, the actual number indicated by the count was 196 per cubic yard or 3920 inhaled per day.

In a later publication COCKE (1938a) put his theoretical calculations to the test by an ingenious device which recorded all the pollen in metered air. He found remarkably close agreement between the measured and calculated values for pollen grains which are approximately spherical when dry. Ragweed pollen he found to be under represented on the slides by 32.2 per cent and pine by 56.2 per cent. In the former the spicules, in the latter the bladders slow up their rate of fall by those amounts. In this paper the author furnishes a table which greatly facilitates the conversion of the number of grains caught into the number present per cubic yard of air, a part of which is reproduced here:

Table for determining the number of pollen grains of a given size per cubic yard of air from the number of grains caught on one square centimeter in twenty-four hours: —

	18 μ	20 μ	22 μ	24 μ	26 μ	28 μ	30 μ	32 μ	34 μ	36 μ	38 μ	40 μ
1	10	7	6	5	4	4	3	3	3	2	2	2
2	19	15	12	10	9	7	6	6	5	4	4	4
3	29	22	18	15	13	11	10	9	8	7	6	5
4	38	29	23	20	17	15	13	12	11	9	8	7
5	48	37	29	25	21	18	16	14	13	11	10	9
6	58	43	35	30	26	22	19	17	16	13	11	11
7	68	51	41	35	30	26	22	20	19	15	13	13
8	78	58	47	40	34	30	26	23	21	18	15	14
9	87	66	53	45	39	33	29	26	24	20	17	16
10	97	73	59	50	43	37	32	30	27	22	19	18

Reproduced from COCKE (1938a)

The method of using the table is simple. For example, if one catches ten grains of ragweed pollen in 24 hours, the grains are 20μ in diameter so he reads 73 in the vertical column but ragweed is slowed 32.2 per cent in its rate of fall by its spicules so he would add about one third of this number which gives a concentration of 97.3 per cubic yard. Of course for larger numbers, multiples of those shown in the first column may be used.

The methods of recording pollen in general use give the grains caught per unit time, generally 24 hours, and do not tell much about the fluctuations of pollen density which may take place from hour to hour during the day. Recently HAWES, SMALL and MILLER (1942) have devised an apparatus with a clock-work mechanism which moves a slide across a jet of metered air which impinges upon it through a slit. In 24 hours' operation it distributes the pollen from about five cubic yards of air along a band one cm wide and 6 cm long, so that the fluctuations in pollen density are continuously recorded.

The techniques for appraising airborne populations of microorganisms, pollen and insects have been reviewed up to 1941 by the Committee on Apparatus in Aerobiology of the National Research Council (ANNAND *et al.* 1941). Other methods and apparatus, particularly those for use in aeroplanes, will be found in their report.

Identification: — By whatever method the atmospheric pollen is caught it must be accurately identified. Some help in this may be had from the author's book, *Pollen Grains* (WODEHOUSE 1935) in which the grains of many species are described and illustrated, also from *Atmospheric Pollen* (WODEHOUSE 1942*b*) which is an atlas containing descriptions and figures of all atmospheric pollen known to the author. But final identification is best made by actual comparison with known material. For this purpose a reference collection of mounted specimens of pollen is necessary. The collection should include specimens of pollen from all anemophilous and as many as possible of the common entomophilous plants of the region under investigation.

Preparation of Pollen Slides: — In order to prepare pollen for microscopic examination a small amount of dried pollen, about as much as can be picked up on the small end of a flat toothpick, is placed on the center of a microscope slide, and a drop of 95 per cent alcohol added. The pollen is then stirred with the toothpick and the alcohol drawn off with a tuft of twisted cotton to remove the oil. If there is much oil on the pollen a second or third application of alcohol is necessary. After all free alcohol has been drawn off, but while the pollen is still moist with it, a very small drop of melted glycerine jelly containing basic fuchsin is added and, keeping the slide warm by passing it several times quickly through a small flame, the pollen is stirred in with the toothpick until it is evenly distributed. Then a No. 0 cover glass is warmed by passing it several times through the flame, while held vertically with the forceps, and pressed lightly onto the preparation. It is of the utmost importance that the preparation be as thin as possible; if the correct amount of jelly has been used it will just reach the

periphery of the cover glass as the latter begins to press the pollen grains against the slide, so that the thickness of the mount is no greater than the diameter of the pollen grains. Slides prepared in this way can be studied with the most powerful oil-immersion lenses, which is essential to reveal their textures and fine sculpturing, and such slides will keep several years, though they are not actually permanent.

If naturally shed pollen is not available suitable material can generally be obtained from good herbarium specimens. To do this a few mature anthers are removed with forceps under a hand lens, placed on a microscope slide and extracted with alcohol as before. Then a large drop of water is added, and brought to a boil by passing the slide several times through the flame. The anthers are then opened with needles under a dissecting microscope and the pollen scraped out. The empty anthers are removed, the water drawn off with a twisted tuft of cotton, a drop of melted basic-fuchsin-glycerine-jelly added and the preparation covered as before. This method is more troublesome than that with naturally shed pollen, but it gives equally good results and possesses a worthwhile advantage in that the pollen preparations may at any time be referred to the exact specimens from which they came, in case the question of identification should arise. For this reason the slide should always be given a number corresponding to that of its herbarium specimen.

Methods of collecting and preserving herbarium specimens are to be found in many botanical textbooks (*e.g.*, BAILEY 1924, SWINGLE 1934) so need not be described here. Suffice it to say that specimens to be used for pollen preparations should be dried rapidly and completely, and in mounting they should be strapped, not glued, to the sheets, or a few extra flowers for dissection may be dried separately and enclosed in little paper packets glued to the specimen sheet.

In the identification of atmospheric pollen it is rarely possible to tell the exact species, but it is generally possible to tell the genus and nearly always the family, and the species can be judged with only a small margin of doubt, by a knowledge of which plants are flowering at the time when the pollen is caught. For example the pollen grains of the grasses are all much alike, except for differences in size, yet if grass pollen is caught on the slides, let us say when sweet vernal-grass is in flower, and the grains which are caught correspond in size to those of sweet vernal-grass, it is reasonably certain that they are of that species. In this way the laboratory and field observations supplement each other.

In general it is found that the symptoms of hayfever sufferers correspond in their appearance and severity with the incidence of the pollen of one or more species of plants in the region (SACK and GOLAN 1942). If pollen samples of these are tested by means of the skin test, their importance or its lack can be ascertained with certainty.

Botanical Literature:—The botany of the flowering plants of North America is well understood and recorded in numerous local manuals and larger works of a monographic nature, covering the entire country. The following list will enable the student of hayfever to select the volumes necessary to the region in which he is working.

The general principles of plant classification may be found in many elementary textbooks of botany (*e.g.*, SINNOTT 1935) but they are more fully treated in the few books which are devoted to the general subject of taxonomy alone. Such a work is that of SWINGLE (1934). The first part of this book sets forth and illustrates the principles on which systematic botany is based; the second describes about sixty families of flowering plants, including some of those of special interest to the student of hayfever. Others which may be mentioned are J. C. WILLIS (1908) which discusses principles of taxonomy and systems of classification, with suggestions to collectors; and HITCHCOCK (1925) which is an excellent guide to plant collection and study. These and other such books are designed to explain taxonomy rather than to serve as taxonomies.

For the identification of plants encountered in botanical surveys it is generally necessary to turn to the standard manuals of botany or local floras. Occasionally one venturing into this field is deterred from the use of these books by the difficulties which appear to confront the uninitiated in the highly technical language in which such books are generally written. They make use of many words which are not encountered in ordinary language, it is true, but these are logical in their meaning, and use in their construction only a few simple roots which occur over and over again, so that the mastery of such words is not difficult after the first few have been learned. Such technical expressions are necessary in the interests of brevity and accuracy; their meanings have been conventionally agreed upon and are restated in the glossaries which accompany most taxonomic works. Rather than be deterred from the use of such books on account of their technical language, one should welcome the sense of security which comes from the use of precise language admitting of no ambiguity. Moreover there is no alternative for those who would understand even the elements of taxonomic botany. Many so-called popular books, written probably honestly, attempt to provide an avenue of escape, excusing their existence by capitalizing the imaginary difficulties and dangers of technical language. But for the hayfever botanist these will be found only a snare for, being written largely for the aesthetic appeal that flowers may make to the dilettanti, they generally omit from discussion the mundane weeds and most other plants of economic importance, devoting their attention to those plants which offer a supposedly more aesthetic appeal through their pretty flowers, of little interest to the student of hayfever. Some even omit entirely the two great hayfever-plant families, the composites and grasses, as being too difficult, which they probably are. For this purpose there are many excellent manuals and floras.

Northeastern United States:—The “New Manual of Botany” (GRAY 1908) is perhaps the most famous of all botanical manuals. It was first published by ASA GRAY of Harvard University in 1848. It has been repeatedly revised and extended, and is now in its seventh edition, revised by B. L. ROBINSON and M. L. FERNALD. The edition is at present out of print but the book is undergoing still another revision under the direction of Dr. FERNALD. The area covered by the present edition extends from Newfoundland to the southern boundary of Virginia and westward along the southern boundaries of Kentucky, Missouri and Kansas to the 96th meridian, including adjacent parts of Canada. It is illustrated with 1036 small figures designed to bring out the technical characters of most families and genera.

“The Illustrated Flora of the Northern United States” by BRITTON and BROWN (1913) is a much larger work than GRAY’s manual, in three volumes with a total of 1652 pages and 4666 illustrations. Practically every species is illustrated, which greatly facilitates their identification. Its area is about the same as that of GRAY’s manual, extending from the Atlantic coast westward to the 102nd meridian and south to the southern boundaries of North Carolina, Tennessee, Missouri and Kansas.

“The Manual of the Flora of the Northern United States and Canada” by N. L. BRITTON (1907) is an unillustrated abridgement of the Illustrated Flora, covering the same area.

Southeastern States:—“Flora of the Southeastern United States” by JOHN K. SMALL (1913) covers the area immediately south of that covered by the Illustrated Flora, including Florida and the Gulf coast, and west to the one hundredth meridian.

The book is now out of print and difficult to obtain but has been largely replaced by "The Manual of the Southeastern Flora" by the same author (SMALL 1933). This book is a great improvement over the earlier volume. Each genus is illustrated by sketches of dissections of representative species setting forth important diagnostic and anatomical features. The area covered, however, is somewhat less extended than that of the earlier volume. It includes the plants which grow naturally south of the northern boundaries of North Carolina and Tennessee and east of the Mississippi River.

For the southeastern region there is the excellent little "Flora of the District of Columbia and Vicinity" by HITCHCOCK and STANDLEY (1916), almost nontechnical but complete.

Central States:— The "Flora of the Prairies and Plains of Central North America" by RYDBERG (1932), as stated in its preface, aims to be a complete manual of the flowering plants and ferns and their allies of the states of Kansas, Nebraska, Iowa, Minnesota, South Dakota, North Dakota, and of southern Manitoba and southeastern Saskatchewan. It includes also most of the species occurring in the prairie regions of Illinois, southern Wisconsin and northern Missouri, and on the plains of eastern Colorado and eastern Montana. The volume is an exceptionally fine piece of work, the last by its great author whose untimely death occurred while the book was still in press. It contains 600 figures illustrating representative species of as many genera.

The state of Kansas is well served by GATES (1936, 1940, 1941), three volumes dealing with the Grasses in Kansas, an Annotated List of the Plants of Kansas and the Weeds in Kansas.

The state of Oklahoma is well served by the Oklahoma Flora by T. R. STEMEN and W. S. MYERS (1937), but from this volume the grasses are omitted.

Rocky Mountain Region:— This region is well served by the Flora of the Rocky Mountains by RYDBERG (1917) covering the states of Utah, Colorado, Wyoming, Idaho, Montana, and adjacent parts of Canada, the Dakotas and Nebraska. The work is a complete flora, unillustrated. The "New Manual of Botany of the Central Rocky Mountains" by COULTER and NELSON (1909) is a revision by NELSON of COULTER'S Manual of Rocky Mountain Botany, 1885. "The purpose has been to use Colorado as the center of the flora included in the manual and to present the complete flora of that state, of Wyoming, of Yellowstone Park, and of the Black Hills of South Dakota; also to include most of Montana, southern Idaho, and the eastern half of Utah, and the northern half of New Mexico and adjacent Arizona". The book, though old, is still serviceable in its area.

Southwest:—"Botany of Western Texas" by COULTER (1894) is the only book devoted to the flora of western Texas. The "Flora of New Mexico" by WOOTON and STANDLEY (1915) is an unillustrated volume, listing without description, all species (2971) known to occur within the boundaries of New Mexico. The distribution of each species within the state and its range outside, and other items of interest to the hayfever botanist are given. "The Flowering Plants and Ferns of Arizona" by KEARNEY and PEEBLES (1942) is an illustrated flora of the state, published by the U. S. Department of Agriculture. It is a splendid volume, complete and authoritative. The section of the *Compositae* is contributed by S. F. BLAKE and that on the grasses by JASON R. SWALLEN, based on HITCHCOCK'S Manual of the Grasses. The "Flora of Utah and Nevada" by TIDESTROM (1925) presents a discussion of the ecological aspects of the region and a systematic list of the flowering plants without description, but giving their distribution and habitats.

Pacific Coast:— The "Illustrated Flora of the Pacific States" by ABRAMS (1923) is designed to be an authentic reference book covering the flora of Washington, Oregon and California, patterned after the Illustrated Flora of the Northern United States by BRITTON and BROWN. When completed it is proposed to fill three volumes. So far, however, only the first volume has been published. It includes such groups of special interest to the student of hayfever, as the grass, willow, walnut, birch, beech, and elm

families. The volume comprises 557 pages with 1299 figures illustrating practically every species described.

The "Manual of the Flowering Plants of California" by JEPSON (1925) is an admirable and extremely useful volume. It comprises 1238 pages with 1023 figures designed to illustrate the important diagnostic features of the species described.

The northern part of the Pacific coast region is covered by several useful books. A "Flora of Northwest America" by HOWELL (1903) describes the plants of Washington, Oregon and western Idaho. Of more restricted range is the "Flora of Southern Washington and adjacent Idaho" by PIPER and BEATTIE (1914). Serving essentially the same region is the more recent and very excellent flora by HAROLD ST. JOHN (1937). The "Flora of the Northwest Coast" by PIPER and BEATTIE (1915) covers the region from the summit of the Cascade Mountains to the Pacific Ocean from the 49th parallel across the northern portion of Vancouver Island to the northern boundary of Lane County, Oregon. The "Flora of the State of Washington" by PIPER (1906) presents "An annotated catalogue of the species of vascular plants of Washington." The species are not described, but their habitat, range and zonal distribution are given. The volume comprises 637 pages with 22 plates, the latter largely of an ecological nature, as are also the first 75 pages, which are devoted to a study of the region.

Cultivated Plants:—It is unfortunate that none of the manuals and floras listed above gives more than passing reference to the cultivated species, since it is among these that one most frequently encounters the minor or incidental causes of hayfever. As we have already seen, the general rule that showy plants do not cause hayfever, can not be applied too strictly to cultivated plants; it is one thing to pass a plant in the field but quite another to handle it, as we are prone to do with cultivated plants, and live with it in the same room. However these are all provided for in a number of very excellent books. The "Manual of Cultivated Plants" by BAILEY (1924) describes the species most commonly cultivated in America, for whatever purpose, and whether outdoors or under glass, accounting for 3665 species in 170 families. Also included are many species formerly cultivated, now abandoned but become more or less well established in the wild. The book comprises 851 pages and 14 full page figures illustrating typical species from some of the families. Though the volume is not otherwise illustrated, it possesses such excellent keys and concise descriptions that identifications are not difficult. The book, however, does not give much consideration to the innumerable horticultural varieties which make the botany of cultivated plants so difficult and complex. These, however, are fully described in that monumental work, "The Standard Cyclopedia of Horticulture" by the same author (BAILEY 1914), accounting for 20,602 species with their varieties. The "Field, Forest and Garden Botany" by GRAY (1895), as revised by BAILEY, is a simple introduction to the common plants east of the 100th meridian. Though both wild and cultivated plants are included the emphasis is on the latter. REHDER (1940), "Manual of the Cultivated Trees and Shrubs Hardy in North America" is a book of 996 pages dealing with the woody plants, unillustrated, but gives the times of flowering and the zones in which the plants are hardy. "The Cultivated Conifers of North America" by BAILEY (1933) is a splendid volume including all species of conifers known in cultivation north of Mexico. The word, 'cultivated', is interpreted in its broadest sense, including many native species which are only occasionally found in cultivation. Thirty-nine genera and 275 species are discussed and 57 others incidentally recorded. The volume comprises 403 pages, 48 plates and 114 other figures. The plates and figures are a delight to behold.

The Trees:—There are many excellent tree books but the greatest of them all, in fact one of the greatest books ever produced in this country is the "Silva of North America" by C. S. SARGENT (1897). The book is in 14 volumes comprising 2185 pages and 740 full-page lithographic plates. Each species is illustrated and described, with notes on its ecology and economic importance. Unfortunately few people can afford the luxury of owning such a book as this, and it is scarcely to be found outside of the larger libraries. An excellent substitute, however, is found in the "Manual of the Trees of North America" by the same author (SARGENT 1922). This is the standard

condensed reference book on trees in this country. It brings into convenient form the materials of the *Silva*. It comprises 910 pages. Each species is fully described, with ecological notes and detailed account of its distribution within its range, which is a valuable feature not found in any of the manuals and floras, which are content to merely outline the ranges. Each species is illustrated, with a total of 783 figures, of more than passing excellence, by CHARLES EDWARD FAXON and MARY W. GILL. Cultivated trees are not treated, only occasionally mentioned in passing. "North American Trees" by BRITTON (1908) deals with the trees growing independently of cultivation north of Mexico. Each species is illustrated and described in almost non-technical language.

There are many tree books of a less technical nature, among which may be mentioned JULIA ROGERS (1905), "The Tree Book, a popular Guide to a Knowledge of the Trees of North America and their uses in Cultivation", and EMERSON and WEED (1918), "Our [American] Trees and how to Know them", an excellent popular book with a good photograph and description of each species.

There are also a number of tree books of limited range, among which should be mentioned the "Handbook of the Trees of the Northern States and Canada east of the Rocky Mountains" by HOUGH (1907). Most of the species described are illustrated to show their habit, leaves, fruit, twigs, and flowers and frequently a section of wood. "The Trees of Texas" by LEWIS (1915) is an illustrated manual of the native and introduced trees of the state. California is well supplied through the several publications of JEPSON of which perhaps the most important is "The *Silva* of California" (JEPSON 1910), a large and complete technical volume well illustrated. The "Trees of California" by the same author (JEPSON 1909) is a small popular manual with many illustrations.

Monographs of Restricted Groups:—Of special interest to the student of hayfever is "The Phylogenetic Method in Taxonomy" by HALL and CLEMENTS (1923). It is a treatise of the North American species of *Artemisia*, *Chrysothamnus* and *Atriplex*. The species are minutely described showing their relationships, distribution, time of flowering and importance in hayfever. A purely taxonomic treatment of *Artemisia* and allied genera has been published in the North American Flora by RYDBERG (1916). Also published in the North American flora is the "*Ambrosiaceae*" by RYDBERG (1922) and "*Xanthium*" by MILLSAUGH and SHERFF (1922) which should be regarded as the standard texts on the tribe *Ambrosieae*.

The "Manual of the Grasses of the United States" by HITCHCOCK (1935) is recognized as the final authority on this group. The book comprises 1040 pages and 1696 figures. The species are fully described, most of them illustrated and accompanied by maps showing their distribution in the United States. A valuable feature of the work is that English names are given for the species as far as these are known or exist, standardized by the late F. C. COVILLE, formerly a member of the American Joint Committee on Horticultural Nomenclature and one of the authors of Standardized Plant names. Both the technical and vernacular names used in this book should be recognized as the standards.

"The Genera of the Grasses of the United States" is a similar but much smaller work by HITCHCOCK (1920). Under the generic headings most economic species are described including practically all those of interest to the student of hayfever.

Of interest to those who wish to follow up the subjects of taxonomy and floristics in greater detail is the recently published "Geographical Guide to the Floras of the World" by BLAKE and ATWOOD (1942). This is an annotated list of all important taxonomic publications throughout the world, with special reference to useful plants and common plant names.

Those who wish to go deeply into the subject of pollen identification will find much useful information in ERDTMAN (1943), Pollen Analysis. Though this book deals primarily with fossil pollen, the principles laid down in it are as readily applicable to the study of atmospheric pollen of the present.

Chapter II

THE HAYFEVER PLANTS — GYMNOSPERMS

The gymnosperms may be distinguished by their seeds which are borne naked on the upper surface of the scales of cones instead of in a closed ovary in a flower. The pollen is borne in little anther sacs on the under surface of scales of smaller cones. In fertilization the pollen is brought directly in contact with the ovule. Almost never are the two sexes combined in the same cones, but the pistillate and staminate cones are borne sometimes both on the same plant, sometimes on different plants.

All species are wind pollinated and many of them are characterized by the enormous quantities of pollen that they shed. Fortunately, however, the pollen of most species is quite harmless in hayfever. The gymnosperms are generally tall stately trees with needle-shaped leaves. But there are some notable exceptions. Some are merely shrubs, like the little mugo pine of parks and gardens; the larches are completely deciduous; the maidenhair tree has broad flat fan-shaped leaves and some of the Southern Hemisphere podocarps have leaves as broad as our ordinary hardwood trees. *Phyllocladus* has all its leaves reduced to scales which soon drop off, their place being taken by specialized flattened branches which are green and function like leaves. Exceptions of this kind, however, are to be expected in a group as old as the gymnosperms. They are the records of the vicissitudes of their ancient past.

The gymnosperms are, indeed, an immensely ancient group. They were represented in past geological ages by such mighty races of trees as the *Cycadofilicales* and *Cordaitales* of the Carboniferous period and the *Bennettitales* of the Mesozoic era. They are today represented by four living groups, the *Cycadales*, including the sago palm and comfort root, the *Ginkgoales*, itself a mighty phylum in past geological ages but of which only the maidenhair tree remains among the living, the *Coniferales*, comprising the pines, firs and larches and in fact all the better known gymnosperms; and the *Gnetales*, a small and poorly understood group of desert and tropical countries, but now famous for *Ephedra* which is the source of the popular drug ephedrin. Of these only the following two families are of interest to students of hayfever.

Ginkgoaceae (The Ginkgo Family)

Ginkgo or maidenhair tree (*Ginkgo biloba* L. or *Salisburia adiantifolia* Sm.) is a large and beautiful tree, generally with tall straight central axis bearing large heavy side branches slanting obliquely upwards. Its leaves are broad and fan shaped, resembling the leaflets of the maidenhair fern.

The trees are dioecious, the staminate and pistillate cones occurring in separate trees. They shed large quantities of light pollen which has occasionally been suspected of causing hayfever.

The pollen grains (fig. 8B) are boat shaped, 27 to 32 μ long, provided with a single deep longitudinal furrow, the exine is thin and smooth. The

primitive character of this grain is entirely in harmony with the position assigned to this species among the most primitive species of living gymnosperms.

Ginkgo is native of Japan and eastern China where it is a favorite tree for planting in the temple gardens. It has been called by DARWIN a "living fossil," for it is the last of a mighty race which flourished in the early and middle periods of the Mesozoic, probably starting their career even as long ago as the Permian in association with the *Cordaitales* and *Cycadofilicales*. This single remaining species is not known to occur in the wild state; indeed it has been said to owe its survival to the fact that for centuries it has been regarded as sacred by the Chinese, and piously planted and cared for by the Buddhist priests. Recently, however, its cultural value has become widely recognized and it is now used as an ornamental tree almost throughout the civilized world.

Coniferae

The family of the *Coniferae* includes trees and shrubs with flat needle-shaped leaves, such as the pines, firs, junipers, and yews. They are mostly evergreen, inhabitants of temperate regions.

The members of the family are most properly grouped into the following tribes: (1) *Araucarineae*, the Southern Hemisphere pines, (2) *Podocarpaceae*, the podocarps and their allies, mostly of the southern hemisphere, (3) *Abietineae*, comprising the pines, firs, spruces and larches, mostly of the north temperate region, (4) *Cupressineae*, including the junipers, cypress and allied forms, (5) *Taxodineae*, including the bald cypress (*Taxodium*) and sequoias, (6) *Taxineae*, including the yews. The six tribes are fairly distinct and such relationships as exist between them are obscure and controversial.

Most species shed enormous quantities of pollen which is notorious for the great distances it is carried by the wind, yet only a few, principally members of the *Cupressineae*, have been shown to cause hayfever. Their pollen, however, is among the most frequent and conspicuous elements caught on atmospheric pollen plates.

Abietineae (The Pines, Spruces and Firs)

On the basis of their pollen grain structure the *Abietineae* may be divided into two, the winged-grained and the wingless-grained. The pollen grains of the winged-grained *Abietinae* (fig. 8A,F,G) are characterized by the possession of a single longitudinal germinal furrow on the ventral side. It is usually only vaguely defined but is generally flanked by two conspicuous air-filled bladders. When the grains are moist they spread apart and expose the furrow, and when they are dry they press tightly together over the furrow as if to check further loss of water. The bladders also undoubtedly serve to give the grains greater atmospheric buoyancy for, in spite of their large size, they are known to be transported great distances by the wind. Generally there are two bladders symmetrically arranged, but occasional grains may be found in the pollen of most species with three, four, or more bladders, and the grains of some of the firs have a single bladder encircling the furrow in the form of a frill. On the other hand the pollen grains of the larches and some of the hemlocks (fig. 8D,E) are without bladders.

Pinus (The Pines)

The pines are all evergreen with needle-shaped leaves fascicled in axillary clusters of one to five enclosed at their base by a membranous sheath. They are monoecious with the staminate cones clustered at the base of leafy growing shoots of the year, small and catkin like, yellow, orange or scarlet, composed of numerous spirally arranged two-celled anthers (fig. 7C).

The pollen grains range from 44 to 65 μ in diameter, exclusive of the bladders. The latter are rounded when expanded, and retain most of their convexity even when tightly closed over the furrow (fig. 8F).



FIG. 7.—Cones of conifers. A, Hemlock (*Tsuga*) pistillate and B, a single scale bearing its two seeds. C, White pine, staminate cone and D, pistillate.

Pine pollen has occasionally been reported to cause hayfever (*e.g.*, WALKER 1921, DAVISON, LOWANCE and DURHAM 1934), but it is doubtful if these cases have been fully substantiated. More recently ROWE (1939) has reported a case of pine pollen allergy which seems to leave no doubt that pine pollen can be allergenic. Significant skin reactions were obtained with this case to the pollens of Monterey, white, knob-cone, Austrian, sugar, bishop, yellow, Scotch and tamarack pines. ROWE states, "Pine pollen allergy productive of bronchial asthma and associated with large scratch skin reactions is recorded for the first time in the literature." Presumably the earlier records are not regarded by him as authentic. The rarity of such cases is in a way surprising for pine pollen is among the most abundant in the atmosphere.

The genus comprises about 70 species, trees and shrubs of the northern hemisphere. The species can be conveniently grouped into two sections, the soft pines and the pitch pines. The former are characterized by soft close grained and light colored wood, their leaves generally in clusters of five. The pitch pines have usually heavy coarse-grained wood, often dark colored, and their leaves generally in clusters of two.

Among the soft pines the best known, and formerly one of the commonest trees throughout eastern North America, is the white or Weymouth pine (*Pinus Strobus* L.). It is a tall timber tree reaching a height of 225 feet, flowering in June.

Among the pitch pines the Jersey or scrub pine (*P. virginiana* Mill.) is the common tree of the pine barrens of New Jersey and Long Island. It is generally a small tree but reaches its best development in the western part of its range, sometimes attaining a height of 110 feet. Flowering in May the trees shed large quantities of pollen.

A species similar to and often associated with the Jersey pine is the pitch or torch pine (*P. rigida* Mill.). It is a small tree reaching a height of only about 80 feet.

In the Rocky Mountain region are a number of very beautiful species which have occasionally been thought to cause hayfever. Among them is the western pitch pine or bull pine (*P. scopulorum* Lemm.). It is a large tree attaining a height of 120 feet with leaves two or three in a cluster. Its seed-bearing cones are dense and woody, their scales thickened towards their ends and tipped with a prickle.

Many of our native pines and several European species appear frequently in cultivation. One of the commonest of the introduced species is the beautiful Austrian pine (*P. nigra* Arnold, *P. Laricio* Poir.). It is a large tree of variable habit, frequently reaching 100 feet in height, with dark green leaves 3 to 7 inches long in fascicles of two. It occurs in several geographical and horticultural forms. One of those most generally cultivated is the variety *austriaca* Asch. & Graeb. (*P. nigricans* Hort.), a broad headed form generally with a flat top. The species is native of southeastern Europe but is widely planted.

Also frequently cultivated in the East is the Scotch pine (*P. sylvestris* L.). It is a large forest tree native of Europe and Asia.

A great favorite, especially for planting around houses and in small gardens, is the little mugo or Swiss mountain-pine (*P. Mugo* Turra., *P. montana* Mill.). It is extremely various, occurring as a low prostrate shrub or as a pyramidal tree reaching 80 feet in height. It is native of the mountains of central and southern Europe, but is extensively cultivated elsewhere, especially in its smaller varieties. It flowers in May shedding fairly large amounts of pollen.

Picea (The Spruces)

The spruces comprise about 40 species of north temperate and sub-arctic regions, of tall pyramidal trees with whorled branches. Their leaves are generally four angled and distributed rather evenly around the twigs.

The pollen grains (fig. 8A) are similar to those of *Pinus*, except that they are larger, ranging in the different species from about 68 to 91 μ in diameter, exclusive of the bladders; also the latter have a tendency to be flattened from below, and when they are pressed together, as the grains dry, they generally become flattened or even concaved on their proximal sides.

Perhaps the best known species, and the one most commonly cultivated, is the Norway spruce (*P. Abies* Karst.), native of Europe. Our commonest native species in the East are the white spruce (*P. canadensis* B.S.P.) and the red spruce (*P. rubens* Sarg.). In the West are found such forms as the Engelmann blue spruce (*P. Engelmanni* Engelm.) and the Sitka spruce (*P. sitchensis* Carr.), and in the Rocky Mountain region the beautiful Colorado blue spruce (*P. pungens* Engelm.).

The spruces are among our commonest evergreen trees, and their pollen is nearly always caught in abundance on pollen slides in May and June, but it has not been shown to cause hayfever.

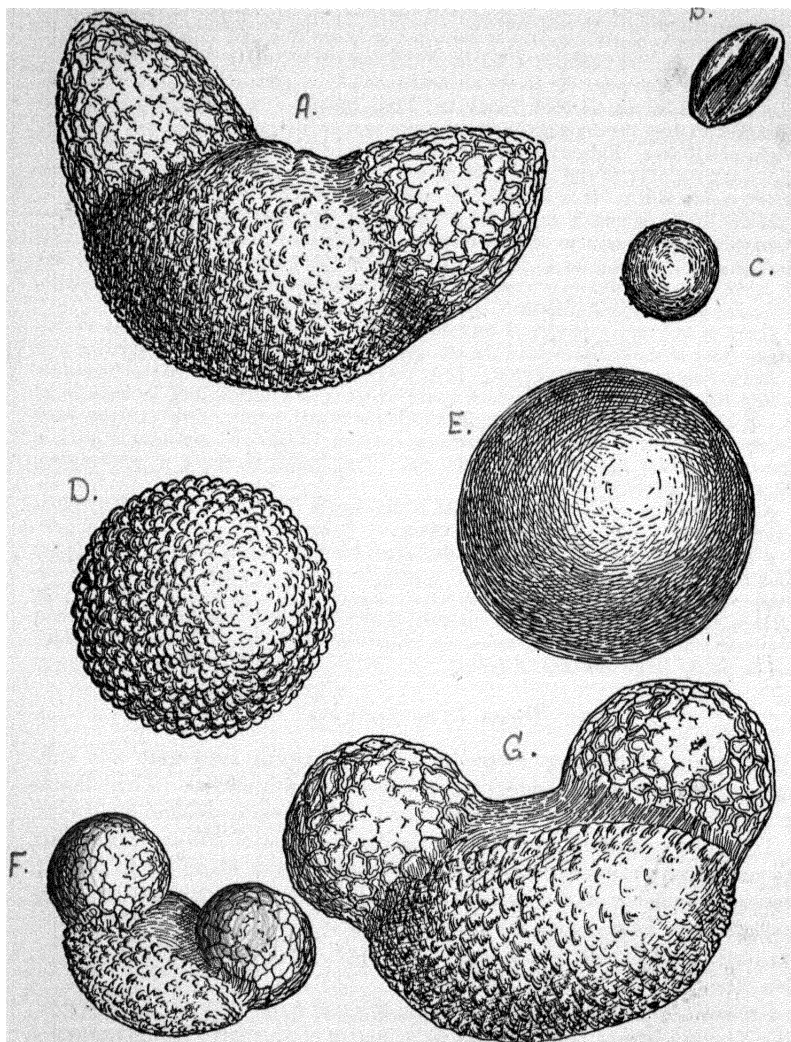


FIG. 8. — POLLEN GRAINS OF GYMNASPERMS: A. Upper left, Spruce (*Picea canadensis*); B. Upper right, Ginkgo (*Ginkgo biloba*); C. Right second from upper, Red cedar (*Juniperus virginiana*); D. Middle left, Hemlock (*Tsuga canadensis*); E. Middle right, Larch (*Larix laricina*); F. Lower left, White pine (*Pinus strobus*); G. Lower right, Fir (*Abies*). All magnified 700 times.

Abies (The Firs)

The firs comprise about 30 species of tall pyramidal trees of north temperate and sub-polar regions, with spreading flat leaves appearing to be two ranked.

Their pollen grains are similar to those of the pines and spruces but larger than either, ranging in the different species from 78 to 101 μ in diameter, exclusive of the bladders (fig. 8G). The large size of these grains restricts their dissemination by wind for they are seldom caught on atmospheric plates, nor is their pollen known to cause hayfever.

Several species are cultivated. The white fir (*A. concolor* Lindl. & Gord.), a native western species, is much used in landscaping. The common or Canada balsam (*A. balsamea* Mill.) is abundant throughout a large part of Canada. On the Pacific coast are several species of particularly beautiful and imposing trees.

Tsuga (The Hemlocks)

The hemlocks are tall pyramidal trees with gracefully nodding leading shoot. The leaves are short and flat, scattered on the twigs but spreading horizontally so as to appear two ranked. The genus comprises about nine species of temperate regions. In America the most widely distributed is the common hemlock (*T. canadensis* Carr.), growing naturally throughout the northeastern United States and Canada. On the Pacific coast are found the western hemlock (*T. heterophylla* Sarg.) and the mountain or black hemlock (*T. Mertensiana* Sarg.), both extending from Alaska to California.

Two types of pollen grain occur among the species of this genus. The grains of *T. canadensis* and *T. heterophylla* are without lateral bladders or have them represented by only a rudimentary frill (fig. 8D), while those of *T. Mertensiana* are generally provided with two well developed bladders causing the grains to resemble those of the firs, but they are smaller, 57 to 65 μ in diameter. The grains of *T. heterophylla* are about 50 to 55 μ in diameter, those of *T. canadensis* 60 to 85 μ . Both are somewhat flattened dorsiventrally, more so on the dorsal than the ventral side. The exine of the dorsal surface is thick and coarsely reticulately corrugated, that of the ventral thinner and merely granular. Frequently the margin at the junction of the two is thrown into a puffy frill suggesting a rudimentary bladder encircling the grain.

Hemlock pollen, in spite of the large size of the grains, is frequently caught on atmospheric pollen slides, and has occasionally been suspected of causing hayfever.

Cupressineae (The Junipers and their Allies)

The *Cupressineae* comprise about seven genera of trees and shrubs, all rather closely related and including, besides the two described below, the Cypress (*Cupressus*), the white cedars or arborvitae (*Thuja*) and the incense cedar (*Libocedrus*). They are distinguished by their small opposite or whorled leaves which are usually scale like, and their small pistillate

cones with few scales. Their pollen grains are spheroidal with thin flecked exine and greatly thickened intine and with only a small and inconspicuous germ pore or none at all.

Since it has already been shown that members of two genera of this tribe cause hayfever, all should be regarded as potential causes until proved otherwise.

Juniperus (Juniper, Savin, Red Cedar)

The junipers are evergreen trees or shrubs usually with thin shreddy bark and small leaves which may be sharp pointed and spreading or scale like and closely appressed. The trees are principally dioecious, though some species are partly monoecious. The staminate cones (fig. 9) are minute,



FIG. 9. — Staminate cone of *Juniperus*.

borne in short axillary or terminal branches from buds formed the previous autumn on branches of the year. The fruit is a berry-like succulent, blue, blueblack or red strobile, containing one to six bony wingless seeds.

Most species produce surprisingly large amounts of pollen which is shed generally very early in spring or, in the milder regions, in mid winter or even late fall.

The grains (fig. 8C) are spheroidal, 20.5 to 30.0 μ in diameter, exine thin and irregularly flecked with granules. Occasional grains are found provided with a single small circular germ pore. The intine is excessively thick and, expanding upon the absorption of moisture, ruptures and throws off the exine, so that cast exines are as often found as intact grains.

The genus comprises about 40 species widely distributed throughout the northern hemisphere. The American species fall into two rather distinct groups or subgenera designated as *Oxycedrus* and *Sabina*. Those of the first group have linear-lanceolate prickly-leaved leaves, arranged in three series, and spreading; and their cones axillary, the pistillate maturing in the third year to form bright blue subglobose berries. These are regarded as the true junipers including, for example, the common juniper (*J. communis*). Those of the second group have mostly scale like leaves arranged in two or three series and closely appressed, except on young plants and vigorous shoots where they may resemble the leaves of the first group, and their cones are terminal on short axillary branches, the pistillate maturing into red, reddish brown, blue or black fruit;

these are the cedars or savins, for example the red cedar (*J. virginiana*). Some authors prefer to treat the two groups as separate genera, in which case *Oxycedrus*, since it is regarded as comprising the true junipers, takes the name *Juniperus*, while the others are called *Sabina*. It is the opinion of the present author, however, that the two groups are too closely related to bear separation into different genera.

The most important in hayfever is the mountain cedar, Mexican cedar or rock cedar (*J. mexicana* Spreng., *J. sabinoides* Nees). It is a small tree, occasionally reaching 100 feet, but generally little more than a large shrub, forming a wide round topped, open and irregular or narrow pyramidal head. This species is extremely abundant on the lime-stone hills of Texas. "The plant is more abundant along the rather rugged escarpment which borders the southern edge of the Edwards Plateau. Here it is very abundant and practically the only juniper" (THARP 1937). The species is generally regarded as dioecious, but Professor THARP states that it is not entirely. "Occasionally one finds a few berries on a staminate tree. I do not recall having noted any staminate cones on a pistillate plant, however". Flowering in December and January, the tree produces enormous quantities of pollen which is known to cause a serious type of winter hayfever. This was first brought to the attention of the medical profession by KEY (1918). KAHN and GROTHAUS (1931) find that in parts of Texas mountain cedar pollen is as important as ragweed pollen is in the East, its effects lasting sometimes eight weeks.

The Texas mountain cedar is an outstanding example of a plant that has been made to cause hayfever by human activity. Of it WILLIS and DEGLER (1939) say, "Some old settlers claim that years ago there were comparatively few cedar trees in Texas, and that the hills were covered largely with high grass. This grassland was used for grazing; over-grazing without giving the land proper rest periods probably gave the cedar growth its start. It then became the practice to burn the grass (and incidentally the cedar) off at definite intervals. As this area became more thickly populated fences were erected; over-grazing became more intense and the danger of burning the fences stopped the practice of burning, until now many of the Texas hills are covered with a very thick growth of cedars".

The common red cedar or juniper (*J. virginiana* L.) also called red savin, Carolina cedar or pencil wood, is the most abundant juniper throughout the eastern United States and Canada, frequenting fields and pastures and dry rocky places. It is generally of a slender columnar form, with fragrant red heart wood. It is naturally variable and has given rise to many cultivated varieties. It flowers very early in spring, about March or April. Its pollen has been shown to interact with that of the Texas species (KAHN and GROTHAUS 1931), and it appears likely to cause some hayfever, particularly in Georgia and Tennessee where the species is most abundant and reaches its best development.

Several other species of Juniper are occasionally encountered in hayfever literature and, since the pollens of all seem to interact more or less perfectly, it is possible that they cause some hayfever. Among these should be mentioned the common juniper (*J. communis* L.) also called horse savin, hackmatack and aiten. It is a shrub or small tree of pyramidal habit, not over 30 feet in height, with leaves all spreading and prickly tipped. It flowers in April or May. Its fruit, the malneat berries of commerce used for flavoring gin, ripen in October. The species is extremely variable and has given rise to several varieties much prized in cultivation.

The cherrystone juniper (*J. monosperma* Sarg.) is a shrub or small tree of southern Colorado, New Mexico, Arizona and Utah, and the alligator or checker-bark juniper (*J. pachyphloea* Torr.) is generally a small tree, 50 to 60 feet high, of Northern Texas, New Mexico and Arizona. Both species flower very early in spring, February or March, and are regarded as possible causes of hayfever in New Mexico and Arizona. The Utah juniper (*J. utahensis* Lemm.) occurring in the Rocky Mountain region and westward to southern California, and the Rocky Mountain juniper (*J. scopulorum* Sarg.) occurring in the Rocky Mountain region and westward to British Columbia, are believed to occasionally cause hayfever.

Of special interest is the Bermuda cedar (*J. bermudiana* L., *J. barbadensis* L., *Sabina bermudiana* Antoine). It is an irregular and widely branched tree, reaching a height of about 70 feet and a trunk diameter of four feet, with thin gray flaky bark. The leaves of young plants and shoots are spreading and sharp pointed but those of mature twigs are scale like and closely appressed in four ranks giving the twigs a four sided appearance. The trees flower in March and April shedding large quantities of pollen which causes almost the only hayfever there is in Bermuda (HODGSON 1935, GAY, CURTIS and NORRIS 1941).

Bermuda cedar is the most abundant tree of Bermuda and apparently does not grow outside of the islands, although it has been reported as growing in the West Indies. A similar and very closely related species, commonly called Cuban cedar (*J. lucayana* Britt.) is found in the northern Bahama Islands and Cuba. This species is also known as *J. barbadensis* Sarg. and *Sabina barbadensis* Small. and appears to be the species referred to by KAHN and GROTHAUS (1930) and reported by them to probably cause some hayfever in Florida.

Chamaecyparis (Cypress and Retinispora)

The cypresses are tall pyramidal trees resembling the junipers. The staminate and pistillate cones are borne on the same tree but on different branches.

The genus comprises about six species, confined to the Atlantic and Pacific coasts of North America, and Japan and Formosa. They are closely related to the junipers but may be distinguished by their woody cones in place of the berry-like fruits of the junipers. They are also closely related to the genus *Cupressus*, another group of cypresses to which the Monterey cypress belongs, but may be distinguished from them by the fact that the cones of *Cupressus* mature only in their second year while those of *Chamaecyparis* mature in their first. Nevertheless the two genera are frequently joined as one under the name, *Cypress*.

There are many varieties, shrubby forms, of both the native and Asiatic species in cultivation known as retinisporas among the horticulturists, using the name of an old genus which included the juvenile stages of *Chamaecyparis* and *Thuja*.

On account of the closeness of their relationship with the junipers it is likely that the cypresses have the same capacity to cause hayfever, but only Lawson cypress or Port Orford cedar (*Chamaecyparis Lawsoniana* Parl., *Cupressus fragrans* Kell.) has been shown to do so. This is a noble forest tree occasionally reaching 200 feet in height, with a pyramidal head of bright green leaves. In its natural habitat it is found only on moist hillsides and canyons in southern Oregon and northern California. It has, however, given rise to many prized varieties which are cultivated throughout the warm moist regions of the United States under such names as cream

cypress, scarab cypress, silver queen and steel cypress. It flowers principally in May, shedding large amounts of pollen which has been shown by BLACK (1929) to interreact perfectly with that of Texas mountain cedar and to be a contributing cause of hayfever.

The pollen grains of Lawson cypress are similar to those of the junipers, but are extremely various in size, 28.6 to 39 μ in diameter ; and generally they exhibit a small germinal papilla. The exine may be almost entirely covered with minute flecks or nearly smooth.

Chapter III

THE HAYFEVER PLANTS — ANGIOSPERMS

The angiosperms may be distinguished by their universal habit of bearing their seeds in closed ovaries instead of naked on cone scales as do the gymnosperms. Their pollen does not come in direct contact with the ovule; instead it is deposited on the stigma and its tube must penetrate the tissues of the pistil to reach the ovule. The fructifications of the angiosperms are

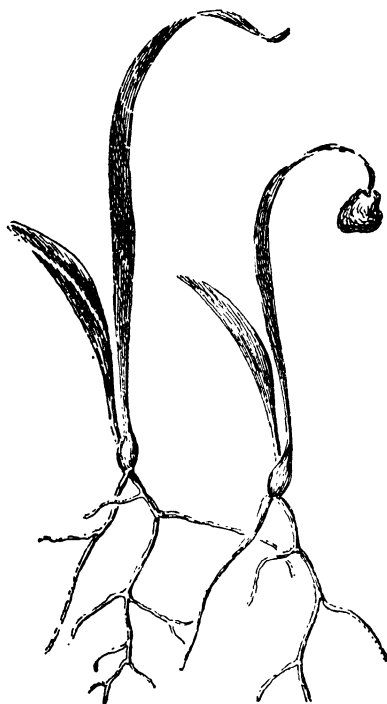


FIG. 10. — Lily (*Lilium*) seedlings,
an example of a Monocotyledon.

true flowers. Basically the flower is a beautiful and attractive structure, and these characters are with it primitive. Witness, for example, the beautiful flowers of magnolia, the water lily or buttercup, all three of which are among the most primitive angiosperms. There appears to be little doubt that the angiosperm flower arose in association with—possibly even as the result of—pollination by insects. It is therefore basically and primitively a mechanism adapted to securing pollination by insects. The wind-pollinated forms are always derivative and never primitive.

The angiosperms are arbitrarily divided into two groups, the monocotyledons and the dicotyledons, so called because the seedlings of the

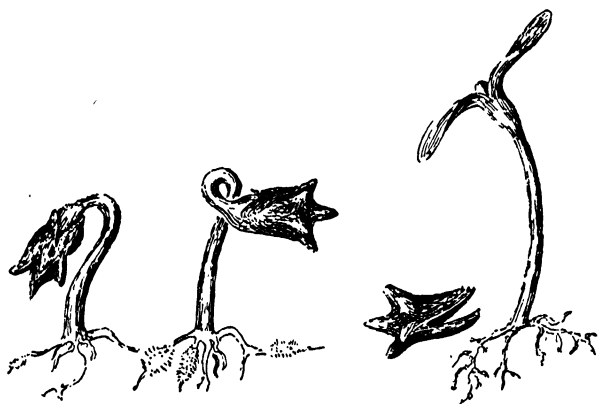


FIG. 11. — Ragweed (*Ambrosia*) seedlings, an example of a Dicotyledon.

majority of the first group seem to produce but a single seed leaf or cotyledon



FIG. 12. — Foliage leaves, examples of Monocotyledons (A,B) and Dicotyledons (C,D): A, *Iris*, B, Day-flower (*Commelina*), C, English ivy (*Hedera*), D, *Chrysanthemum*.

(fig. 10) while the seedlings of the majority of the second group produce two cotyledons (fig. 11). There are many exceptions, and among the more

primitive members of the groups the dividing line is seen only vaguely and has given rise to much controversy. For the most part, however, the two groups are quite easily distinguished and appear to be at least partly natural. The monocotyledons generally have parallel veined leaves, like those of the palms, iris and grasses, while the dicotyledons generally have net veined leaves, like these of the oak, lilac and chrysanthemum (fig. 12). The dicotyledons may form a cambium in their stem, a thin-growing layer which builds up a fresh layer of wood and bark each year, as in the oaks, poplars and maples. Monocotyledons never do; for example the palms are unable to enlarge their trunk diameter no matter how tall they grow. The prevailing form of pollen grain among the monocotyledons has a single germinal furrow or pore, except where it has suffered effacement through reduction in response to special modes of pollination (fig. 14). The pollen grains of the dicotyledons generally have three or more pores or furrows, except the reduced forms which have none; only among some of the more primitive members do they have a single one. There are other rules and other exceptions but, for the most part, a little experience will enable one to say at a glance to which of the two groups any flowering plant belongs. The palms, sedges, lilies, grasses and orchids are examples of monocotyledons, while the magnolias, buttercups, maples, roses, oaks and ragweeds are examples of dicotyledons.

Monocotyledons

To this group belong the cattails, sedges, rushes, palms and grasses which are described below, also such well known forms as the lilies, onions, trillium, fritillarias and yucca which belong to the lily family; and their close relatives, the amaryllis, agave and narcissus of the amaryllis family; and the orchids. These are the most typical monocotyledons, but the group also includes the calla, arum, jack-in-the-pulpit and skunk cabbage of the arum family; the water plantains and arrowheads of the water-plantain family; and the pondweeds, naiads, eel grass and quillworts of various other families, so divergent in form and habit that their association with the other members of the monocotyledonous group appears to be arbitrary and unnatural. However, such aberrant forms are of little interest to the student of hayfever because they are either insect pollinated, or they shed too little pollen.

Typhaceae (The Cattail Family)

Typha (The Cattails or Cattail Flags, fig. 13)

The cattails are marsh or aquatic herbs with round stems and long flat leaves sheathing at the base. The flowers are minute and densely crowded into terminal spikes, the staminate in the upper and the pistillate in the lower part of the spike. The flowers themselves are of the simplest structure, the staminate consisting of two to seven stamens surrounded by bristles which represent a degenerate perianth, and the pistillate similar but with a single pistil in place of the stamens. It is this simplicity of floral structure that has condemned these plants to the lowly position assigned them in most classifications, at the very bottom of the monocotyledonous

group. This simplicity, however, is not of a primitive character but due to reductions, the sort that always accompany the habit of wind pollination among the angiosperms, to which the cattails are very well adapted.

The genus comprises about 10 species of temperate and tropical regions. Two of them, the broad-leaved and narrow-leaved cattails (*T. latifolia* L. and *T. angustifolia* L.), are common throughout most of North America except the extreme north. The two species are similar but the former is more robust. Its leaves are one quarter to one



FIG. 13. — Cattail flag (*Typha latifolia*), an example of a Monocotyledon.

inch broad, its flowering spikes dark brown with the staminate and pistillate portions contiguous. It is the more abundant of the two. The narrow-leaved species is more slender throughout and its leaves one third to one half inch broad, its flowering spike light brown, with the staminate and pistillate portions separated by a short naked interval of the stem.

Both species shed enormous quantities of pollen which may be caught on pollen slides miles from where the plants are growing, but it appears to be incapable of causing hayfever. The pollen grains of both are essentially alike except that those of the broad-leaved cattail always occur united in tetrads (fig. 14 E), while those of the

narrow leaved species are always single (fig. 14 F). The individual grains in either case are spheroidal or variously irregular in shape, 18 to 30 μ in diameter, with thin finely reticulate exine and rather thick intine. There is always a single germ pore of irregular shape and with jagged margins. In the pollen of the broad leaved species all possible arrangements of the four cells occur. When the tetrads are flat or squarish the pores tend to be all on the same side of the group and toward the outer margins of the cells, in the tetrahedral tetrads they tend to be on the part of each cell remote from its contact with its neighbors of the group.

Arecaceae (The Palms)

Some of the palms are suspected of causing hayfever. Though they appear to be primarily insect pollinated, there is no doubt that the pollen of some may at times become atmospheric. DAVISON, LOWANCE and DURHAM (1934) pointed out that the date palm (*Phoenix dactylifera* L.), the coconut palm (*Cocos nucifera* L.) and the cabbage palm (*Sabal*) are found in Miami, Florida, and they state, "In Florida and possibly along the southern coast states, the palms produce sufficient pollen to be considered as possible causes of hayfever and hay asthma but we have not been able to find reports of any cases caused by this pollen".

PRINCE (SELLERS 1934), reporting from Galveston, Texas, states, "Another plant with which we must deal . . . is the date palm, a tropical tree that has no definite pollinating season. A great number of these trees occur in our vicinity, and I am told there are several closely related varieties. It is possible to collect as much as half an ounce of very fine light pollen from a single date bloom". There are about a dozen species of date in cultivation. One of the commonest ornamental species in the South is the Canary Island date (*Phoenix canariensis* Chaub.).

Gramineae (The Grass Family)

The grasses are herbaceous or rarely woody plants, with hollow or solid stems, and two-ranked parallel-veined leaves consisting of two parts, the lower enveloping the stem as a sheath, and the upper expanding as the blade. The flowers are generally perfect, that is producing both stamens and pistils, but without functional calyx or corolla, of an inconspicuous greenish color, and aggregated in spikes or panicles at the ends of the main stem or branches. A few, like the Indian corn, are monoecious with the staminate flowers in the tassels at the top of the stem and the pistillate in the axils of the leaves lower down on the stem, or like the Indian rice in which the spatial orientation is reversed, the pistillate flowers being borne at the top of the panicle and the staminate lower down in the same panicle.

The pollen grains of the grasses, when moist and expanded, are spheroidal, ovoidal or ellipsoidal, about 20 to 100 μ in diameter, though seldom over 50 μ (fig. 14). The exine is always thin and nearly smooth, but may be faintly granular or exceedingly finely reticulate pitted, and is almost free from oil. The intine is thick and hyaline. The grains have always a single small germ pore approximately circular in outline, provided with a thickened rim and a minute operculum which, in the moistened condition, stands off from the rim on the bulging pore membrane. When the grains dry the

exine collapses irregularly, generally causing the grain to assume an angular form, and the operculum is drawn tightly into the mouth of the pore.

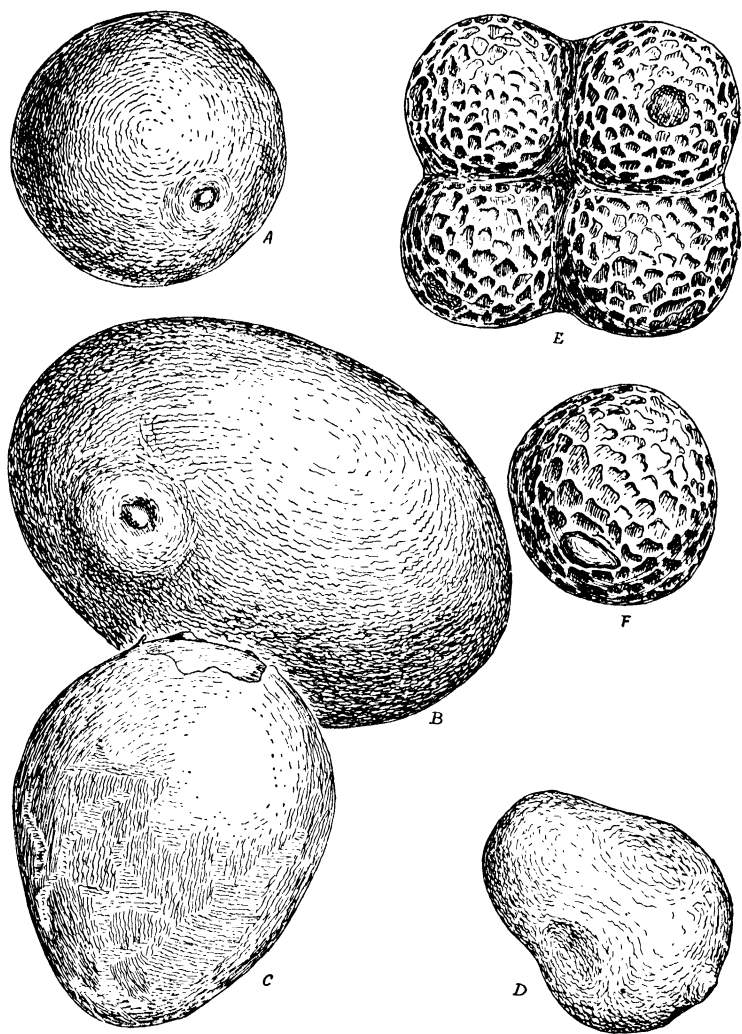


FIG. 14. — POLLEN GRAINS OF GRASSES, SEDGES AND CATTAIL: A, Timothy (*Phleum pratense*); B, Rye (*Secale cereale*); C, Sedge (*Carex*); D, Timothy dry; E, Broad-leaved cattail (*Typha latifolia*); F, Narrow-leaved cattail (*T. angustifolia*). All magnified 1300 times.

The grasses are entirely wind pollinated unless self pollinated, and their flowers are most profoundly modified in adaptation to anemophily. So far reduced are they that it is not easy to make comparison between these flowers and those of more typical

monocotyledons. The flowers are arranged in spikelets of one or several flowers on a short and slender axis which is called the *rachilla* (fig. 15). At the base of the spikelet is a pair of scales called the *glumes* enclosing the structures above them; just above the second glume is a similar structure, the *lemma*, which often has a long slender pointed *awn* growing from its tip. In the axil of the lemma the flower is borne. The outer perianth is a two-keeled scale, the *palet*. The stamens and pistil lie between the palet, which is on the inside, and the lemma which is on the outside. The inner perianth consists of two tiny scale-like *lodicules* between the lemma and the ovary. The stamens are generally three, occasionally one, two or six. Their anthers are borne on long slender filaments which carry them outside of the glumes at maturity. There is one pistil with a single ovule but a study of its development shows that it is composed of three fused carpels. There are generally two styles or occasionally three.

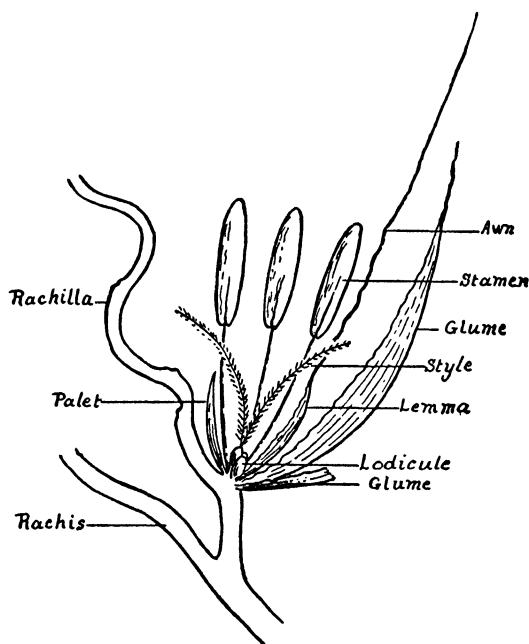


FIG. 15. — Spikelet of wheat (*Triticum*), partly diagrammatic.

The grass family comprises about 4500 species growing anywhere and in any kind of soil that is capable of supporting vegetation, and even in water. About 1100 species are native or naturalized in North America, and among them are counted some of our worst hayfever plants. The pollen of most, if, indeed, not all species appears to be capable of sensitizing hayfever patients so that the governing factors in their production of hayfever are primarily their abundance, the amount of pollen set free, and its range of dispersal. In these there is an enormous variation among the different species. Fortunately, by far the majority of grasses are relatively harmless. Some species are wholly or in part self pollinating, the flowers remaining completely closed or only opening partly for a short time. Thus some of the panic grasses and rice cutgrass (*Leersia oryzoides*) are self pollinating without opening at all, while the florets of wheat expand for a short time, when cross pollination may take place, but for the most part are self pollinating. Such cases, however, are not the rule; the majority are cross

pollinated but do not shed enough pollen to be important in hayfever. A relatively small number of species account for practically all the grass hayfever. In the eastern part of the United States these flower for the most part in the spring or early summer. The most important, named in order of their seasonal appearance, are: sweet vernal-grass, June grass, orchard grass, appearing in May and early June, and timothy, redtop and the various closely related bentgrasses, appearing in June and July. Other species, somewhat less important but which frequently contribute their quota of pollen during one or the other or both of these periods, are red fescue, meadow fescue, quack grass, ryegrass, darnel and velvet grass. Of course there are many others which contribute to some degree, but all so much less important that it is rarely necessary to give them serious consideration in handling hayfever cases.

Most of the species already mentioned are grasses of cultivation, consequently are widely distributed. In fact they are found wherever the climate is humid and cool. In the warm and more arid regions other grasses take their places. Thus Bermuda grass extends from coast to coast through the southern states. On account of its wide range and long flowering period, lasting throughout the growing season, this is perhaps the most important hayfever grass of North America. Frequently associated with Bermuda grass in the arid parts of its range is Johnson grass which may be in some places almost as troublesome as Bermuda grass, but its distribution is much less extensive and its pollen grains are very large, which materially restricts their range of dispersal.

On the Pacific coast ryegrass assumes a position of some importance and in the arid and semi-arid regions of the western interior some of the brome grasses. In fact each floristic region has its roster of grasses. Still when these are all added up their total, though impressive in itself, is small when compared with the 1100 species native or naturalized in the United States, or with the 4500 species distributed throughout the world. Fortunate, indeed, we are that they are not all to be counted as contributing to hayfever.

Certainly not even all the species enumerated in the following pages are causes of hayfever. I have, however, included all that are known to me to have been reported in the literature with any justification as causing hayfever or even with hayfever possibilities, though I fear that some of them have been reported as the result of excessive zeal and insufficient study on the part of their discoverers. The relative importance or lack of importance of many of these will only become known through further study and careful consideration of all the factors concerned, such as the abundance of the plants, the amount and character of their pollen.

The interrelationships of the grasses are somewhat obscure, and even the best classifications are admitted to be partly artificial. It seems certain, however, that the different genera and species are more closely related to each other than is usual in such large families. If other evidence were lacking, this is strongly suggested by the work of the allergist, for he finds that a patient who is sensitive to the pollen of one species of grass is almost invariably sensitive in some degree to all the grass pollens to which he has been exposed, though he may be entirely negative to all pollens except those of grasses. Occasionally it appears that a grass hayfever patient may not be sensitive to the pollen of species to which he has not been exposed, but in such cases a few years exposure is generally all that is necessary to induce sensitization (*cf.* p. 194, also STULL, COOKE and BARNARD 1936 and WALKER 1921).

For the classification of the grasses of the United States, as now arranged, we are all very much indebted to the late Dr. A. S. HITCHCOCK, first, for his "Genera of the Grasses of the United States" (HITCHCOCK 1920), secondly, for his Manual of the Grasses of the United States (HITCHCOCK 1935). It is this latter work that I follow in so far as the taxonomy of the grasses is concerned.

The family is divided more or less arbitrarily into 14 tribes of which only ten include species which are of interest to the student of hayfever. The tribes *Bambuseae*, *Zoysaceae*, *Oryzaceae* and *Melinideae* are not represented here because they do not include plants which can justifiably be considered causes of hayfever.

Tribe 1. **Festuceae****Bromus** (The Brome Grasses)

The bromes are annual or perennial grasses with terminal open or contracted panicles of large spikelets. Some of the native perennial species, and the introduced European smooth brome, are important forage grasses in the mountainous regions of the western United States. The annual species are mostly weedy. Some of them are useful range grasses but others are serious pests since their barbed fruits work into the eyes, nostrils and mouth of stock, causing serious injury.

Their pollen grains are spheroidal or ovoidal, generally uniform in size, about 40 to 48.5 μ in diameter, their germ pore 3.4 to 6.3 μ in diameter, and with finely granular or faintly reticulate exine (fig. 14).

The genus comprises about 60 species of which about 36 are native or naturalized in the United States. Most of them shed relatively little pollen and are not regarded as serious causes of hayfever, though they may occasionally constitute a contributing factor in some regions of the western states.

Smooth or Hungarian brome (*B. inermis* Leyss.) is a perennial European species cultivated in America for hay and pasture especially in the western states, now running wild almost throughout. It flowers in June and July but is not an important factor in hayfever though occasionally regarded as such. California brome (*B. carinatus* Hook. & Arn.) is an erect annual or biennial with smooth or slightly hairy leaves and large spreading panicles. It is common in open ground, open woods and waste places at low and middle altitudes along the Pacific coast, extending into British Columbia, Idaho, through Montana to New Mexico. It appears to be rather an important cause of hayfever in the Pacific states, in the early summer, varying widely in its flowering period in different localities. The species merges with the large mountain brome (*B. marginatus* Nees) from which it can only be distinguished arbitrarily. This latter is an annual or short-lived perennial with broader spikelets than in the previous species, otherwise similar and to be regarded as a variant of it.

Chess or cheat (*B. secalinus* L.), also known as rye-brome and cock-grass, is a perennial weed, adventitious from Europe, in grain fields and waste places more or less throughout the United States, but it sheds so little pollen that it is of little or no importance in hayfever. Soft chess or brome (*B. mollis* L.), also called haver, hooded, bull, lob or lop grass, is an erect annual, 8 inches to 3 feet high, softly pubescent throughout. It is a weed, adventive from Europe, in waste places almost throughout the United States and Canada, except far south. It is particularly abundant on the Pacific coast where it is believed to be a contributing factor in hayfever, flowering in June and July. In hayfever literature and elsewhere it is frequently but incorrectly referred to as *B. hordeaceus* L.

Ripgut grass (*B. rigidus* Roth) is a common and troublesome weed, and probably an important cause of hayfever in the Pacific coast states, especially southern California (Rowe 1929), flowering from May to July. It is distinguished from the other bromes by its larger awns which sometimes cause the ripened spikelets to be injurious to stock.

Festuca (The Fescues)

The fescue grasses are low or rather tall, mostly tufted, annuals or perennials, with spikelets in narrow or open panicles. Their pollen grains are spheroidal, or ovoidal with the germ pore at the large end, 31 to 36.5 μ in diameter. The pore is approximately circular but with wavy margin, 2.5 to 4.5 μ in diameter.

The genus comprises about 100 species, of which about 34 are native or naturalized in the United States. Many of the perennial species are important forage grasses in the grazing sections of the West and some, such as sheep and red fescue, are cultivated as lawn and pasture grasses in the East. Several constitute a serious menace to hay-fever sufferers.

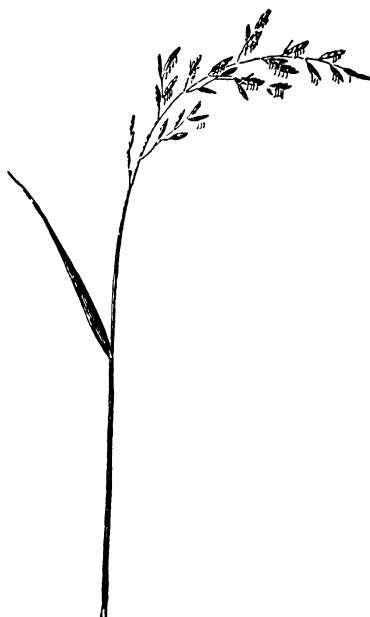


FIG. 16.—Meadow fescue (*Festuca elatior*), flowering stalk.

Meadow fescue (*F. elatior* L., *F. pratensis* Huds., fig. 16), also called tall fescue, English bluegrass, Dover grass, Randall or evergreen grass, is slender, 2 to 5 feet high, with smooth simple stem and panicle 4 to 14 inches long. It is a variable species introduced from Europe and cultivated for hay and pasture and naturalized throughout the cooler parts of the United States and Canada, in meadows, roadsides and waste places. It flowers in June and July and is known to cause hayfever.

Red fescue (*F. rubra* L., fig. 17) is a tufted perennial with smooth stems rising from creeping rhizomes, 1½ to 2½ feet tall, and panicles 2 to 5 inches long, sometimes tinged with red. Most of the leaves are basal forming a tuft, and are involute filiform, but the few on the stem are short

and flat. It is native of Eurasia but now widely distributed in the cooler parts of the northern hemisphere. It flowers principally in June and July and is a moderately important cause of hayfever.

Sheep fescue (*F. ovina* L.), also called black twitch-grass, is similar to red fescue but may be distinguished by its generally more erect habit. It appears to be adventive from Europe, but is now widely distributed in fields and waste places throughout the United States and Canada, except the extreme south. It flowers in June and July and is a contributory cause of hayfever.

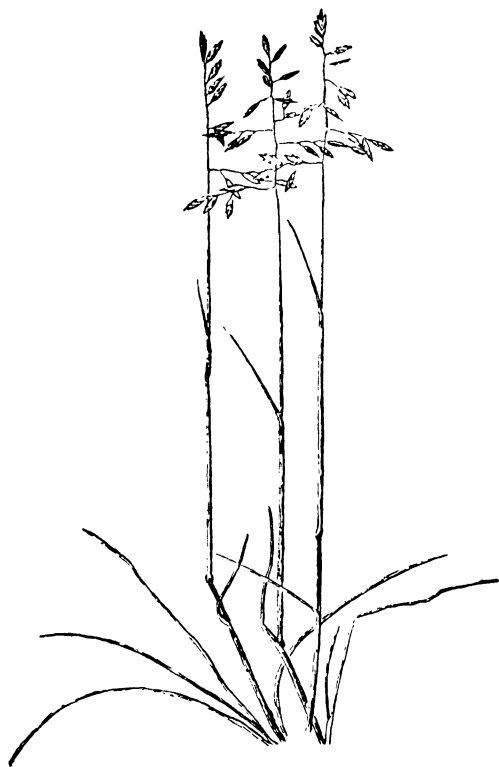


FIG. 17. — Red fescue (*Festuca rubra*), flowering stalks.

Poa (The Bluegrasses)

The bluegrasses are low or moderately tall slender perennials, or occasionally annuals, bearing open or contracted panicles, and narrow and generally flat leaf blades. Their pollen grains are approximately spheroidal, 22.5 to 32μ in diameter, with the germ pore more or less irregular in shape, and capped by a small operculum which is likewise irregular, and exine

rather coarsely granular as compared with that of the pollen grains of other grasses.

The genus comprises about 150 species, widely distributed in all temperate and cold regions. About 64 occur naturally in the United States. Nearly all are palatable to stock; some are cultivated for pasture and others form a large part of the forage of mountain meadows in the West. Still others are used as lawn grasses.

One of the commonest species is annual bluegrass, low spear grass, dwarf or meadow grass (*P. annua* L., fig. 18). It is a low tufted, generally prostrate grass spreading and rooting at the nodes and often forming mats, or occasionally it may assume a more erect form. It is native of Europe but naturalized throughout North America, except in the most arid regions, in open ground, lawns, pastures, waste places and openings in woods. It flowers practically throughout the growing season, in the warmer regions even during the winter. In the northeastern states the bulk of its flowering takes place very early, usually in April, before that of sweet vernalgrass,



FIG. 18. — Low spear or annual bluegrass (*Poa annua*).

and before grass hayfever-cases begin to manifest symptoms. It is, therefore, safe to say that it is of little importance in hayfever in spite of its abundance. This is probably due to the fact that it liberates very little pollen.

Canada bluegrass (*P. compressa* L.), also called wire grass, flat-stemmed meadowgrass and English bluegrass, is a low perennial with slender creeping rhizomes and bluish green erect stems, bearing narrow panicles. It is naturalized in America from Europe, now widely distributed often in poor soil in open grounds, open woods, meadows and waste places throughout most of Canada and the northern United States. The plants shed large amounts of pollen which is a serious cause of hayfever from June to August.

June grass, Kentucky bluegrass, or common meadow grass (*P. pratensis* L., fig. 19) is one of the most important hayfever grasses of the United

States. It is a slender perennial, 1 to 3 feet high, from a creeping rhizome, with spreading panicles and narrow flat leaves. It is native of Europe but thoroughly naturalized in America, and extensively cultivated for lawns and pastures in the more humid and northern parts of the United States and adjacent Canada. Escaped from cultivation it is distributed almost throughout the United States except in the arid regions; it is not common in the Gulf states. It flowers in May and June, at about the same time as

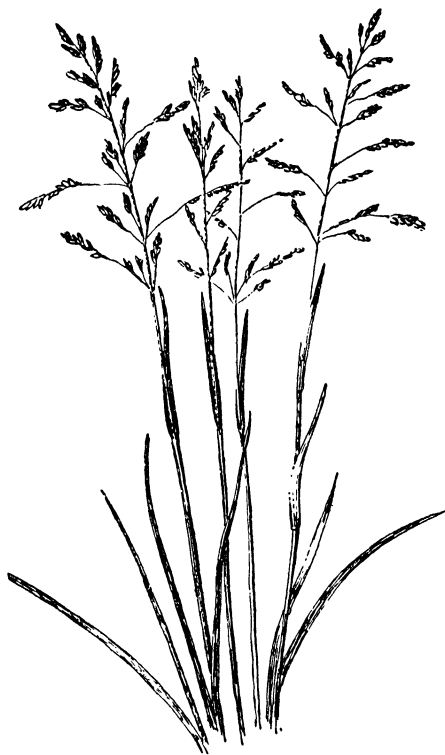


FIG. 19. — June or Kentucky bluegrass (*Poa pratensis*).

orchard grass, with which it is often associated, the two together accounting for most of the hayfever which occurs during the first half of the grass-hayfever season in the East.

Rough bluegrass or rough-stalked meadow grass (*P. trivialis* L.) is a rough-stemmed perennial, erect from a decumbent base but without creeping rhizomes. It is adventive from Europe in the northeastern United States and on the Pacific coast in moist places. It may occasionally be an important contributing cause of hayfever but in hayfever literature is not generally distinguished from Kentucky bluegrass.

Saltgrass (*Distichlis spicata* Greene), also called marsh spike grass and alkali grass, is a low perennial from extensively creeping rootstock, with rigid stems, rigid convolute leaves and contracted panicles of large, smooth, flattened spikelets, the staminate and pistillate flowers borne on different plants. Their pollen grains are uniform, spheroidal or ovoidal, 31 to 34 μ in diameter.



FIG. 20. — Orchard grass (*Dactylis glomerata*), three flowering stalks.

Saltgrass is common in salt and tidal marshes along the Atlantic, Gulf and Pacific coasts as far north as Nova Scotia and British Columbia. Flowering from June to September, it is believed to be a contributory cause of hayfever.

Orchard grass (*Dactylis glomerata* L., fig. 20), also called cocksfoot, dew or hard grass, is a tall perennial with flat leaves and spreading panicles, composed of smaller heads of spikelets, generally forming large tussocks. Its pollen grains are spheroidal or ellipsoidal, 28.5 to 38.8 μ in diameter.

Orchard grass is adventive from Europe or Asia, now abundant throughout the United States and Canada. It favors moist situations and partial shade, hence is frequently used in orchards as a ground cover. It is also commonly cultivated as a meadow and pasture grass. As a cause of hayfever it is one of the most important in the United States, shedding its pollen in May and June at about the same time as June grass with which it is often associated.

Tribe 2. **Hordeae**

Agropyron (The Wheatgrasses)

The wheatgrasses are perennials, often with creeping rhizomes, and usually erect stems and erect green or purplish spikes. Their pollen grains are oval, spheroidal or ellipsoidal, about 45 to 52 μ in diameter, with exine very finely and rather indistinctly granular, the pore approximately circular, with smooth margins and small generally excentric operculum, 5.7 to 8 μ in diameter.

The genus comprises about 50 species, in all temperate regions. About 23 are native or naturalized in the United States. Most furnish forage and a few are among the valuable range grasses of the western states.

Quackgrass (*A. repens* Beauv.) is a wiry grass, 1 to 4 feet high, from long jointed running rootstocks, with spikes 2 to 8 inches long, narrow and flattened. It is naturalized from Europe and now extremely common in fields and waste places almost throughout North America except the extreme north and is often a troublesome weed. It is known by many vernacular names such as quitchgrass, twitchgrass, witchgrass, and couchgrass, and locally by other names as stroil, quichens, wickens, and shelly, knot, dog, shear, slough and pond grass, bluejoint, false wheat and Colorado bluegrass. It flowers from July to September, and is undoubtedly a contributing factor in hayfever but, in spite of its great abundance and wide distribution, it is only of secondary importance because it produces only a small amount of pollen.

Bluestem or western wheatgrass (*A. Smithii* Rydb.) is a pale green glaucous perennial, 1½ to 4 feet high, from a slender creeping rootstock. It is usually found in moist alkaline soil from Manitoba and Minnesota to British Columbia, south to Missouri and Texas. It flowers in June and July and is believed to be an important contributory cause of hayfever.

Wheat (*Triticum aestivum* L., *T. vulgare* Vill., *T. sativum* Lam.) is a low or tall strict grass with flat leaf blades and terminal thick spikes. Its pollen grains are irregular in shape but tend to be ovoidal with the germ pore at the large end, 48 to 57 μ in diameter, the pore generally irregular in outline, 6.3 to 9 μ in diameter; the exine finely but distinctly granular.

Wheat occurs in cultivation in many different varieties, flowering in early summer but, though it is perhaps the commonest grass in cultivation, it is a negligible cause of hayfever because of its marked tendency to self pollination.

The genus comprises 10 species of southern Europe and western Asia. Of these einkorn or one-grained wheat (*T. monococcum* L.) is sparingly cultivated in Europe

and rarely in America. Emmer (*T. dicoccum* Schrank) is occasionally cultivated in America as a forage plant. For a further discussion and bibliography of the wheats the reader is referred to HITCHCOCK (1920, 1935), for a classification of the varieties grown in the United States to CLARK and BAYLES (1935).

Hordeum (Barley)

The barleys comprise about 20 species widely distributed in both hemispheres. Besides the cultivated barley, which appears to be harmless in hayfever, there are about 7 species found growing wild in the United States, some of them weeds with hayfever possibilities. Foxtail barley (*H. jubatum* L.) is a perennial tufted grass with decumbent base and nodding spikes. It occurs in open ground, meadows and waste places almost throughout the United States, except the southern states, and is a troublesome weed believed to have hayfever possibilities in the western states. Mouse barley (*H. murinum* L.) also called wall barley, way bent, squirrel tail, barley grass, foxtail and wild barley, is a similar plant, adventive from Europe, common on the Pacific coast, Idaho and British Columbia, south to Utah, New Mexico and California. Neither sheds enough pollen to be important in hayfever.

Lolium (Ryegrass)

The ryegrasses are annuals or perennials with flat leaf blades and terminal spikes. Their pollen grains are spheroidal or ovoidal with the germ pore at the large end, 30 to 37.6 μ in diameter, the pore approximately circular, 2.8 to 5 μ in diameter, with a relatively small operculum, and the exine faintly granular or reticulate.

The genus comprises about six species, native of the Old World, mostly valuable meadow grasses. Four of these have been introduced into the United States for use as meadow and lawn grasses.

Perennial ryegrass or raygrass (*L. perenne* L., fig. 21), also called red ray, ever grass, red darnel, red dare, English bluegrass, and English ryegrass, is a short-lived perennial, erect or decumbent at the base, $\frac{1}{2}$ to 2 $\frac{1}{2}$ feet tall, with slender arching flattened spikes. It is cultivated in meadows, pastures and lawns, and escaped in waste places almost throughout North America, except far south. It flowers in July and August shedding large amounts of pollen which is a serious cause of hayfever in some regions. It has even been stated by SELFRIDGE (1920) to be "The most important hayfever producer of all the grass family on the Pacific Coast".

Italian ryegrass (*L. multiflorum* Lam., *L. italicum* A. Br.), also called rye grass or wintergrass, is similar in most respects to perennial ryegrass, except that its pollen grains are slightly larger, about 37.5 μ in diameter, and is of similar distribution. It flowers from June to August, and is moderately important in hayfever.

Darnel (*L. temulentum* L.), also called poison or bearded darnel, or Ivray is an annual, 2 to 4 feet high, erect, simple and smooth. Its pollen grains are various, spheroidal, ovoidal or ellipsoidal, 29.5 to 37.6 μ in diame-

ter, with pore 4 to 5.1μ in diameter, and exine finely granular. It is occasionally found as a weed in waste places and cultivated fields almost throughout the region east of the Mississippi River, and on the Pacific coast. Flowering from June to August, it appears to be a contributory factor in hayfever.

Rye (*Secale cereale* L.) is a tall annual grass with flat leaves and simple stems. Its pollen grains are ellipsoidal, 53 to 57μ long and 38 to 43.5μ broad, with the germ pore on the side and towards one end, about 5.7μ in



FIG. 21.— Perennial ryegrass (*Lolium perenne*), flowering stalks.

diameter, circular with a relatively small operculum. This is one of the few kinds of grass pollen grains that can always be readily identified; its large size together with its ellipsoidal form and one-sided placement of the pore are distinctive for this species. Rye is more commonly cultivated in Europe than in America, but here it is frequently escaped in fields and waste places. It is not native of America, probably coming originally from southern Asia. It flowers from May to June shedding prodigious quantities of pollen which is undoubtedly the cause of some hayfever, especially in Europe. The large size of its pollen grains, however, greatly restricts its effective range.

Tribe 3. **Aveneae**
Avena (The Oats)

The oats are annual or perennial with usually flat leaves and terminal panicles. The genus comprises about 50 species, widely distributed in temperate regions, chiefly in the Old World. Several species and hybrid varieties are cultivated for hay and grain. Their pollen grains are generally ovoidal with the germ pore at the large end, 54 to 62 μ long, the pore circular or slightly irregular in outline, 4 to 8 μ in diameter, its operculum about half as broad. The exine is distinctly and rather coarsely granular.

Wild oat (*A. fatua* L.) is an erect glabrous annual, 1 to 4 feet tall, with



FIG. 22. — Velvet grass (*Holcus lanatus*), flowering stalks.

large and loose panicles of mostly three-flowered spikelets. It is adventive from Europe in fields and waste places in the United States, rare in the East but abundant on the Pacific coast where it is regarded as an important cause of hayfever, flowering from July to September. Slender wild oat (*A. barbata* Brot.) is a similar species but more slender and with mostly two-flowered spikelets. It is a common weed of the Pacific coast states and Arizona where it is regarded as a contributory cause of hayfever. The cultivated oat (*A. sativa* L.) is a glabrous annual, about 3 feet high, differing from *A. fatua* in having smaller and two-flowered spikelets. It is cultivated in every state and much of Canada, but more especially in the north central

states or "corn belt", but it is not a factor in hayfever because it is generally self pollinated. For a discussion of the different varieties of oat in cultivation see STANTON (1929).

Velvet grass (*Holcus lanatus* L., *Nothololcus lanatus* Nash, fig. 22) is grayish velvety pubescent, $1\frac{1}{2}$ to 3 feet tall, erect, or decumbent at the base. Its pollen grains are spheroidal, 29.5 to 34μ in diameter, the pore circular or irregular, about 3.4μ in diameter, the exine very faintly and finely granular. The grass is adventitious from Europe, occasionally cultivated on light sandy soil in fields, meadows, and waste places almost throughout the United States east of the Mississippi River, except far south, and on the Pacific coast. It flowers from June to August and is a contributing factor in hayfever in regions where abundant, and is said to be important in California and Oregon. It is called by various names in different places, such as meadow or woolly soft-grass, velvet mesquite, old whitetop, feather grass, and in England, where it is an important cause of hayfever, is known as Yorkshire fog.

Wild oatgrass or poverty oatgrass (*Danthonia spicata* Beauv., *Avena spicata* L.) is a tufted erect perennial, 1 to $2\frac{1}{2}$ feet tall, with narrow leaves and small terminal panicles. Its pollen grains are spheroidal, 28 to 35μ in diameter, the pore circular, about 5.2μ in diameter and with a small generally irregularly shaped operculum, and exine finely but distinctly reticulate granular.

It occurs in dry soil almost throughout the United States and adjacent Canada, except the arid Southwest. It flowers from July to September but is not believed to be important in hayfever.

The genus comprises about 100 species of warm and temperate regions, principally of South Africa.

Western June grass (*Koeleria cristata* Pers., *K. gracilis* Pers.), also known as Koeler's grass, crested hair grass and prairie June grass, is a slender, low or moderately tall caespitose perennial with narrow leaves and shining spike-like panicles. Its pollen grains are spheroidal, 27.4 to 28μ in diameter, the pore generally irregular in form, about 3.4μ in diameter, exine finely granular. This species occurs on prairies, in open woods and sandy soil almost throughout the United States and adjacent parts of Canada and Mexico, except the southeastern states, also in Europe. It flowers from July to September, and is said to be an important cause of hayfever in the western part of its range, e.g., Oregon (CHAMBERLAIN 1927) and Wyoming (SCHEPPEGRELL 1917a).

The genus comprises about 20 species in the temperate regions of both hemispheres. *K. cristata* is the only one native to the United States. *K. phleoides* Pers., a small annual species has been introduced from Europe and is found sparingly in a few localities on the Atlantic and Pacific coasts.

Tribe 4. Agrostideae

Meadow foxtail (*Alopecurus pratensis* L.) is an erect perennial, 2 to 3 feet tall, with compact spikes, 2 to 4 inches long and about $\frac{1}{4}$ inch thick, resembling timothy. This species was introduced into America from Europe as a meadow grass. It is now rather widely distributed in the

northeastern United States and Canada and in Oregon, but not generally abundant. It flowers from May to June and is probably a contributory cause of hayfever in the few regions where it is abundant, possibly in Massachusetts. It may be distinguished from timothy by its habit of flowering several weeks earlier.



FIG. 23. — Timothy (*Phleum pratense*), three flowering stalks.

Timothy (*Phleum pratense* L., fig. 23) or Herd's grass is an erect short-lived perennial, 2 to 4 feet tall, with elongate compact inflorescence several times longer than broad. Its pollen grains (fig. 14 A, D) are spheroidal, 32 to 36.5 μ in diameter, the pore circular or somewhat irregular, 1.7 to 2.8 μ in diameter, and its operculum very irregular, sometimes fragmentary, the exine finely but distinctly granular.

Timothy is native of Europe and northern Asia, commonly cultivated in America and Europe. It is the most important meadow grass in America, and is found escaped in fields and waste places throughout the United States. "The region of the United States most favorable to the growth of timothy . . . is the cool humid region which includes the northeastern portion west



FIG. 24. — Redtop (*Agrostis alba*), flowering stalks.

to the Great Plains and south to Virginia and Missouri, also on the Pacific coast from northern California to Puget Sound". It flowers during June and July, shedding enormous quantities of pollen which is one of the worst causes of hayfever in the early summer.

The genus comprises 10 species in temperate regions of both hemispheres. Four are found in the United States, but of these only mountain timothy (*P. alpinum* L.) is native.

Redtop or Herd's grass (*Agrostis alba* L., fig. 24), also called whitetop or creeping bent grass, is erect, or decumbent at the base, 2 to 4 feet high from creeping perennial rhizomes, with open, usually reddish panicles. Its pollen grains are spheroidal, 26 to 31.2 μ in diameter, their pore approximately circular, 2.3 to 4.6 μ in diameter, with a small generally irregularly shaped operculum, the exine finely but conspicuously granular. "Redtop is cultivated as a meadow and pasture grass in the northern United States and Canada, especially upon acid soils and those too wet for timothy". It is naturalized from Europe but is now established almost throughout North America. It flowers from June to July at about the same time as timothy shedding prodigious quantities of pollen which together with that of timothy causes most of the hayfever occurring during the second half of the grass hayfever season in the East.

The genus comprises about 100 species distributed throughout the world, especially in temperate regions. Thirty-two, mostly adventive species from Europe, are found in the United States. Most of them are valuable forage plants; colonial bent (*A. tenuis* Sibth.) is used for pastures, lawns and golf courses; creeping bent (*A. palustris* Huds.), velvet bent (*A. canina* L.), and Washington bent and metropolitan bent, which are forms of *A. palustris*, are coming into use for lawns and golf greens. These and other species of bent grass appear to be allergically indistinguishable from each other or from redtop. All flower in the early part of summer shedding large quantities of exceptionally buoyant pollen which is the cause of much hayfever.

American beachgrass (*Ammophila breviligulata* Fern.), also called sea-sand reed, sea-mat weed, marram grass, sea marram, is a tough coarse perennial with hard scaly creeping rhizomes, long, tough involute blades, and dense spike-like panicles. Its pollen grains are spheroidal, ellipsoidal or ovoidal, 34 to 39 μ in diameter; pores nearly circular, about 3.4 μ in diameter, with a small irregularly shaped operculum which is even sometimes fragmentary. The American beachgrass is an important sand binder extensively used to arrest drifting sand dunes on Cape Cod and along the Atlantic coast from North Carolina to Newfoundland, also along the shores of the Great Lakes. On the Pacific coast, possibly also partly along the Atlantic, its place is taken by the very similar European beachgrass (*A. arenaria* Link) which has also been successfully used as a sand binder. Both species flower late in summer, June to September, shedding rather large amounts of pollen which probably contributes locally to hayfever.

Tribe 5. Chlorideae

Bermuda grass (*Cynodon Dactylon* Pers., *Capriola Dactylon* Ktze., fig. 25), also called scutch grass, wire grass, Bahama grass, is a low perennial with creeping rhizomes, short leaf blades and several slender digitate spikes at the summit of the upright flowering stems. Its pollen grains are spheroidal, 34 to 35.5 μ in diameter, with rather coarsely granular exine.

Bermuda grass is widely distributed in the southern states from coast to coast, where it is used as a lawn and pasture grass and in some places cut for hay. It is particularly abundant in the irrigated regions of the arid Southwest and is a troublesome weed in much of the semiarid region. It flowers almost throughout the growing season which, in the warmer parts of its range, extends over a period of eleven months. As a consequence of its extraordinary abundance and wide distribution, and the copiousness

and buoyant nature of its pollen, it is perhaps the worst hayfever grass in the United States. It is stated by some authors to be native of the Bengal region of India, by others of southern Europe or the Mediterranean region. At any rate it is "Common in open rather dry ground in the warmer parts of both hemispheres, apparently introduced into America" (HITCHCOCK 1936). From whence or when it came to America seems to be uncertain,

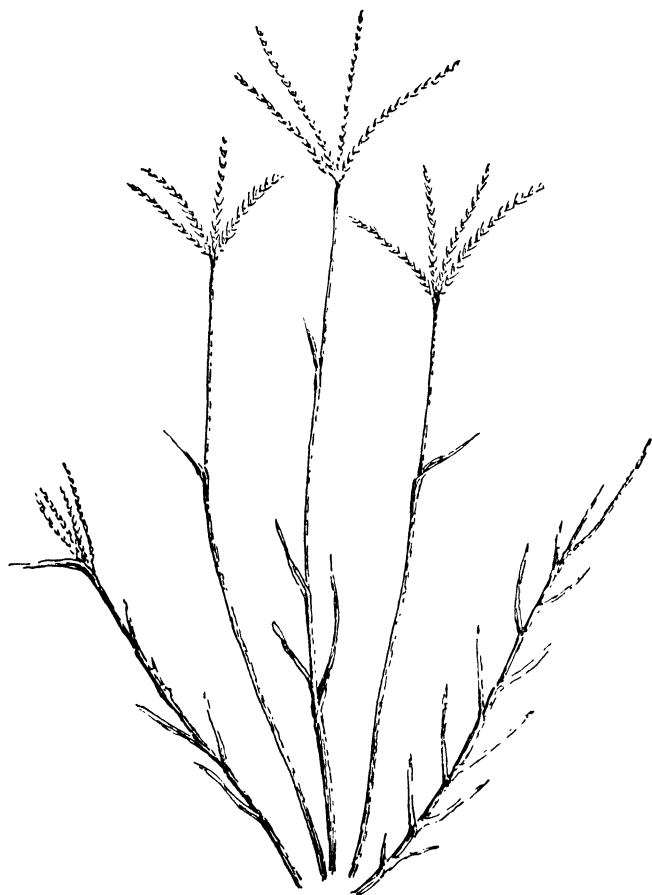


FIG. 25. — Bermuda grass (*Cynodon Dactylon*).

but THOMMEN (1931) states that, "as early as 1807 it was described by JAMES MEASE in his Geological Account of the United States, as follows: 'probably as important a grass as any in the southern states is Bermuda grass, which grows with great luxuriance and propagates with astonishing rapidity by means of its numerous jointings, every one of which takes root'".

A larger form which is found along the coast of Florida has been called *Cynodon maritimus* H.B.K. but appears to be only a form of *C. Dactylon*. Three other species are included in this genus but these occur only in Australia.

Bouteloua (The Gramas)

The gramas are perennial, or sometimes annual, stoloniferous or cespitose grasses with several to many spikes arranged in unilateral racemes. The genus comprises about 38 species, chiefly North American, 18 in the United States, and these constitute one of the most important groups of native pasture grasses in the northern prairie region forming a large part of the "buffalo-grass formation," originally covering thousands of square miles. In distribution the genus extends from Saskatchewan and Manitoba southward between the Mississippi River and the Continental Divide. The western border crosses the Divide in Wyoming and extends into the southern Great Basin region and strikes the Pacific coast at about the Mexican border (GRIFFITHS 1912).

Several species are mentioned in hayfever literature as possible causes of hayfever, but they are all modest pollen shedders and not likely to be of much importance. Indeed the destruction of these grasses and their replacement by various kinds of weeds is responsible for much hayfever.

Blue grama (*B. gracilis* Lag., *B. oligostachya* Torr.), also called mesquite or buffalo grass, is a tufted perennial with numerous short leaves and two or three one-sided spikes about an inch long, one at the top and the other one or two a short distance down the stem. Its pollen grains are spheroidal, 34.2 to 38 μ in diameter, with an irregularly shaped germ pore, 3.4 to 3.7 μ in diameter, and exine of finely and faintly granular texture.

This species is found in the Great Plains from Manitoba to Mexico and southward to South America. Along with buffalo grass it constitutes most of what is known in the Middle West as "Short Grass". It flowers from July to September and in places where still abundant may be a contributory cause of hayfever of slight importance. Other common species are hairy or black grama (*B. hirsuta* Lag.) of about the same distribution as *B. gracilis* and similar in appearance; side-oats grama (*B. curtipendula* Torr.), the tallest species sometimes reaching 3 ft. and further distinguished by its numerous reflexed spikelets, in its range extending further east, even reaching Connecticut; black grama or woollyfoot (*B. eriopoda* Torr.), a low creeping species of Arizona and New Mexico; Rothrock grama (*B. Rothrockii* Vasey) which is the most important range grass in many parts of Arizona; sixweeks grama, which really includes at least two species, *B. barbata* Lag., a low tufted annual, and *B. Parryi* Griffiths, an annual resembling Rothrock grama, both of the Southwest. In hayfever studies distinction is seldom made between the different species.

Buffalo grass (*Buchloë dactyloides* Engelm., *Bulbilis dactyloides* Raf.) is also closely related to the gramas, and often associated with them. It is a low stoloniferous gray-green perennial with curly leaf blades, forming dense sods. It is dioecious, the staminate culms slender, 2 to 8 inches high, the pistillate spikelets mostly 4 or 5 in a short spike. This is one of the most important native American grazing grasses of the dry plains region from Canada to Mexico between the Mississippi River and the Continental Divide, and in New Mexico and Arizona. "It is dominant over large areas on the uplands of the Great Plains, colloquially known as 'short grass

country'. . . . The sod houses of the early settlers were made mostly from the sod of this grass" (HITCHCOCK 1935). It grows on both heavy and sandy soils and before its widespread destruction through agriculture was important in holding such soils against wind erosion. It flowers in June and July but appears to be unimportant in hayfever. This and blue grama have recently been shown by SAVAGE (1935) to possess the highest resistance to drought of any native American grasses.

Saltmeadow cordgrass (*Spartina patens* Muhl.) is a common grass of salt marshes and sandy meadows along the coast from Quebec to Florida and Texas, and in saline marshes inland, New York and Michigan. It often forms compact masses in pure stands along the Atlantic coast where it is cut for marsh hay. It flowers in August and has been suspected of causing some hayfever. Though it is only a moderate pollen shedder it grows in such abundance in some places that it seems possible that it may occasionally be a minor cause of late summer hayfever.

The genus of cord grasses comprises about 7 species widely distributed in salt marshes and are important soil builders in coastal and interior marshes. Apparently, however, none is important in hayfever.



FIG. 26. — Sweet vernalgrass (*Anthoxanthum odoratum*).

Tribe 6. **Phalarideae**

Sweet vernalgrass (*Anthoxanthum odoratum* L., fig. 26) is a fragrant perennial with flattened leaves and spike-like panicles. Its pollen grains are spheroidal, 37.5 to 45.6 μ in diameter, the germ pore variously irregular, 4 to 6.3 μ in diameter and with a small and irregularly shaped operculum, the exine of a faintly granular texture. It is a common weed introduced from Europe in fields, meadows and along roadsides almost throughout the eastern part of Canada and the United States east of the Mississippi River, and on the Pacific coast from northern California northward. In the northeastern part of the United States this is the first important grass to flower in the spring, following closely annual bluegrass, about the first week in May, and continuing until the end of June. It is unquestionably one of the most important hayfever grasses throughout a large part of its range.

The genus comprises four species native of Europe and Asia, of which only the present species has become established in the United States.

Mediterranean canary grass (*Phalaris minor* Retz.) is an annual 1½ to 2½ feet high, with broad leaves and short spikes or almost capitate inflorescence. Its pollen grains are spheroidal, 36.5 to 38.5 μ in diameter, the pore approximately circular, 3.2 to 4.6 μ in diameter, with a small and irregularly shaped operculum, and exine of faintly granular texture. This grass was introduced from Europe, and now occurs sparingly in Louisiana and Texas, but more abundantly in California where it flowers in August and has occasionally been suspected of causing hayfever, though it sheds too little pollen to be of much importance.

The genus comprises 10 species, native of southern Europe and the southern United States. Reed canary grass (*P. arundinacea* L.) is native of North America and is cultivated in the Pacific coast sections of Washington and northern California for hay and pasture. Canary grass (*P. canariensis* L.), a source of canary seed, is introduced from the Mediterranean region throughout most of the United States but is seldom abundant. None of the species can be regarded as important in hayfever though some are occasionally mentioned in the literature.

Tribe 7. **Zizaneae**

Indian rice, wildrice or water oats (*Zizanea aquatica* L., *Z. palustris* L.) is a tall graceful aquatic annual with long flat leaves and a large terminal panicle bearing pistillate flowers on its upper branches and staminate on the lower. Its pollen grains are spheroidal, 34.2 to 40 μ in diameter, with the pore circular, about 4.5 μ in diameter, and a small and irregularly shaped operculum. This grass is abundant in swamps and slow streams throughout the eastern half of the United States and Canada. It flowers from June almost to the end of summer, producing a fairly large amount of pollen, but appears to be unimportant in hayfever.

The genus comprises only two other species; one *Z. texana* Hitchc., is similar in appearance but perennial, native of Texas, the other native of eastern Asia.

Tribe 8. **Panicaceae**

Natal grass (*Tricholaena rosea* Nees) is an annual or short-lived perennial, tall, slender and upright, with beautiful fuzzy purple panicles, 4 to 10 inches long. Its pollen grains are uniform, spheroidal, 34.5 to 41.5 μ in diameter, with a germ pore 4 to 4.6 μ in diameter, its operculum about 3.4 μ

in diameter both nearly circular, and with exine finely and faintly granular. This grass is adventive from South Africa and cultivated as a meadow grass on sandy soils in Florida and to a lesser extent along the Gulf coast. It is sometimes used as a ground cover in citrus groves in Florida, and in many places has assumed the status of a weed along roadsides, grasslands and sandy fields, often so completely occupying these as to turn large sweeps of land a brilliant purple with its beautifully colored panicles. It is, however, only a sparse pollen shedder and, though its rôle in hayfever is not fully understood, there is no concrete evidence to suggest that it is more than a minor and local contributor to hayfever.

Crabgrass (*Digitaria sanguinalis* Scop., *Syntherisma sanguinalis* Dulac), also called hairy finger grass, crowfoot or pigeon grass, is an erect or decumbent annual often rooting at the lower nodes, 1 to 3 feet high, with flowers in 3 to 10 racemes digitate at the top of the stem, appearing late in August and September. Its pollen grains are spheroidal, 32 to 39 μ in diameter, the pore approximately circular, 3.4 to 4.6 μ in diameter with a small irregularly shaped operculum, and the exine coarsely and distinctly granular. This grass bears a strong superficial resemblance to Bermuda grass, and is sometimes mistaken for it by students of hayfever. The two may readily be told apart, however, by simply pulling them up; crabgrass is annual with fibrous roots, whereas Bermuda grass is perennial with an extensively creeping rhizome. Moreover crabgrass is generally much larger and coarser than Bermuda grass, and is tinged more or less with purple, especially as it grows old. It is native of Europe, but now a troublesome weed in waste places and cultivated ground almost throughout the United States. It does not produce enough pollen to be of any importance in hayfever in spite of the great abundance of the plants.

St. Augustine or short grass (*Stenotaphrum secundatum* Ktze.), also called running crabgrass, is a low creeping stoloniferous perennial with short flowering stalks, distinguished by their thick corky rachis in which the spikelets are imbedded along one side. It occurs in moist, especially mucky, soil, near the sea shore, from South Carolina to Texas. It is native of the southern states and tropical America, and is common in the West Indies and Bermuda. It is one of the best grasses for forming lawns in warm tropical climates, and is much used for that purpose in the Gulf coastal towns, particularly in Florida. It flowers almost continuously and has been suspected of causing hayfever, but it is unlikely to be a factor of importance.

Paspalum (The Paspalum or Bull Grasses)

Paspalum is a genus of over 300 species widely distributed in the warmer parts of both hemispheres. Of these about 42 are native or naturalized in the United States and two appear to have hayfever possibilities. Dallis grass (*P. dilatatum* Poir.), also called water grass and tall bull grass, is a tall perennial, 2 to 4 feet high, with erect stems, leafy at the base bearing a lax panicle of three to five spreading racemes of spikelets arranged in twos on the outer side of a dilated rachis, and fringed with long silky white hairs. It is native of South America, recently introduced into the United States and cultivated as a pasture grass in the southeastern states. It now occurs in low ground from rather dry prairie condition to marshy meadows, from

New Jersey to Tennessee and Florida west to Arkansas and Texas. It flowers from early spring to late fall, and is believed to be a contributory cause of hayfever. PENFOUND, EFRON and MORRISON (1930) point out that it is one of the most abundant grasses in the vicinity of New Orleans, rating it second to June grass.

Vasey grass (*P. Urvillei* Steud., *P. Vaseyanum* Scribn.), also called hairy bull grass, is similar to Dallis grass but with a larger and more compact panicle of 10 to 20 racemes. It also comes from South America, introduced from Argentina as a pasture grass in the southeastern states. It is now escaped and found in fields and low places in the coastal plane area from Florida to Texas, and South Carolina. Its rôle in hayfever is not fully understood, but there seem to be grounds for supposing that it has hayfever possibilities.



FIG. 27. — Johnson grass (*Sorghum halepense*).

Tribe 9. **Andropogoneae****Sorghum**

The sorghums are mostly tall annuals or perennials with long flat leaves and large terminal panicles. Their pollen grains are spheroidal, large, 40 to 57 μ in diameter, with a circular or somewhat irregularly shaped germ pore, 3.4 to 5.1 μ in diameter, with a large operculum also generally somewhat irregular in shape and excentrically placed on the pore membrane, the exine finely and distinctly granular. There appears to be no difference between the pollen grains of the several species and their numerous varieties which are encountered in hayfever studies. The genus comprises about 10 species, widely distributed in temperate and tropical regions. Of these only the following two have been introduced into America.

Johnson grass (*Sorghum halepense* Pers., *Holcus halepensis* L., *Andropogon halepensis* Brot., fig. 27), also called evergreen or Egyptian millet, is an erect perennial with extensively creeping rootstock, 3 to 5 feet tall, simple or sometimes branched, smooth, with open panicle, $\frac{1}{2}$ to 1 $\frac{1}{2}$ feet long. This grass was introduced into the United States from the Mediterranean region as a forage plant in the arid regions on account of its drought-resisting qualities, but it has escaped and spread throughout most of the warmer part of the United States, extending from New Jersey and Pennsylvania to Iowa and Kansas, south to Florida and Texas, and west to southern California, and now is a common weed in open ground, fields and waste places. It flowers from July to September, and throughout its effective range which almost coincides with that of Bermuda grass, is believed to be the cause of much hayfever.

Sorghum (*Sorghum vulgare* Pers., *Holcus Sorghum* L., *Andropogon Sorghum* Brot.) is similar to Johnson grass, but annual and generally larger. It originated in Africa but has been cultivated since pre-historic times. Like most plants old in cultivation, it occurs in many varieties differing widely in appearance and the uses to which they may be put. Of those which have reached America, some have received varietal names, and some are even regarded as distinct species, but most are poorly defined and perhaps inconstant. Many of them produce sufficient pollen to cause them to be worthy of consideration in hayfever studies, but there is no need to differentiate between the varieties. The sorghums are cultivated in America chiefly in the regions from Kansas and Texas to North Carolina, for forage and for the juice which is made into syrup. They have not become established as Johnson grass has, and scarcely sustain themselves outside of cultivation. They flower late in summer, for the most part from July to September. Sudan grass (var. *sudanensis* Hitchc.) is similar to Johnson grass, except for its annual habit and greater height. It is extensively grown for hay and pasture. This is perhaps the most distinct variety, and is even sometimes regarded as a distinct species going by such names as *Sorghum sudanensis* Stapf and *Holcus sudanensis* Bailey. Other varieties encountered in American literature are Kafir, Shallu, Durra, Broomcorn and Sorgho.

Tribe 10. **Tripsaceae**

Maize or Indian corn (*Zea Mays* L.) is a robust monoecious annual, 3 to 12 feet high, unbranched but often with prop roots springing from the lower nodes. The staminate flowers are borne in long spike-like racemes forming a large spreading terminal panicle, the "tassel", the pistillate

flowers borne in the ears in the axils of the lower leaves, their greatly elongate styles forming the "silk". The pollen grains are approximately spherical, 80 to 100 μ in diameter, the pore circular, 6.8 to 9.1 μ in diameter, its operculum very irregular, 2.3 to 3.4 μ in diameter, frequently represented by an aggregation of more or less distinct fragments on the pore membrane. The texture of the exine is finely but distinctly granular. This is apparently the largest of all the grass pollen grains.

Maize is one of the most important economic plants of the world. It is cultivated throughout the United States and most of Canada. Its pollen is known to be toxic to hayfever patients and is at times a cause of hayfever, but the large size of the grains prevents it from becoming atmospheric in the sense that that of ragweed and most of the hayfever grasses is. The genus comprises only this species, though occurring in many varieties. It is known only in cultivation, appearing to have originated among the American aborigines on the Mexican plateau in prehistoric times.

Cyperaceae (The Family of the Sedges and Spike-rushes)

These are grass-like or rush-like herbs, with slender solid stems, generally angular, rarely cylindrical, and narrow leaves similar to those of the grasses but with generally closed sheaths. Their flowers are inconspicuous and greenish or brownish arranged in spikelets, adapted to wind pollination.

The family comprises about 75 genera and more than 3000 species of mostly marsh or aquatic herbs. Many species shed enormous quantities of extremely buoyant pollen, which is caught on pollen slides in considerable abundance throughout most of the summer. Nevertheless they appear to be of little if any importance in hayfever, though several have been recorded as possible causes. To this family belong the papyrus of Egypt (*Papyrus antiquorum*), the umbrella plant (*Cyperus alterniflorum*), also a native of Africa now a common pot or porch plant, the spike-rushes (*Eleocharis*) and the true bull rushes which are species of the genus *Scirpus*.

Carex (The Sedges)

The sedges are perennial grass-like herbs with three-angled stems and three ranked leaves, monoecious or dioecious with inconspicuous greenish flowers. The pollen grains (fig. 14C) of the two following species are pear shaped, about 38 μ broad, with a single irregularly shaped and poorly defined germ pore at the large end, and thin exine of granular texture, and irregularly thickened intine with deep inward protrusions on the sides of the grain. When dry the grain is polyhedral, generally tetrahedral.

The genus comprises over 1000 species widely distributed, most abundant in temperate zones, many of them common in bogs and moist places, a few in light dry sandy soil. Some of them shed much pollen which has been occasionally suspected of causing hayfever (ELLIS and ROSENDAHL 1933). Tussock sedge (*C. stricta* Lam.) is a tall smooth and dark green perennial generally growing in dense clumps, abundant in swamps throughout the eastern half of the United States and Canada. It flowers in April and May, shedding much pollen which is frequently caught on atmospheric pollen slides. *Carex pennsylvanica* Lam. is a low grass-like herb with creeping stolons, abundant in dry soil throughout the northeastern part of the United States and Canada. It flowers from April to June, when its pollen may be caught on atmospheric pollen plates.

Nutgrass (*Cyperus esculentus* L.) also called galingale, chufa and nutrush, though it is neither a grass nor a rush. It is a low tufted sedge with extensive slender rootstocks bearing edible nut-like tubers. It is a pernicious weed of gardens, along paths and sidewalks, and along streams especially in sandy soil. It is native of Europe but completely established in the United States from Virginia to Florida and westward to Texas, sparingly elsewhere. It has occasionally been suspected of causing hayfever though this has not been demonstrated. Since it has the characteristics of a hayfever plant in its abundance and the buoyant nature of its pollen it deserves further investigation in regions where abundant.

Juncaceae (The Family of the True Rushes)

The rushes are grass-like usually tufted herbs with flat or round leaves, generally with compound inflorescence, and the flowers scattered along the branches, or in dense heads, their perianth inconspicuous, whitish, greenish, yellowish or brownish, consisting of three chaffy sepals and three chaffy petals. In their floral structure the rushes are thus much less reduced or divergent from the general monocotyledonous form than the grasses, but like the grasses they are entirely wind pollinated. The family comprises about 300 species in 8 genera, of wide distribution, two of the genera represented in North America. Rush pollen is frequently caught on atmospheric pollen slides, but is not known to cause hayfever. All those which I have examined shed pollen only sparingly.

The common wood rush (*Juncoides campestre* Ktze., *Luzula campestris* DC.) is a low herb with densely tufted stems, 4 to 20 inches high, bearing 2 to 4 leaves, their blades flat and tapering to a gland-like blunt point, sparingly webbed when young. The pollen grains of the wood rush (fig. 31A) are uniform in shape and size, always united in groups of four tetrahedrally arranged, the four grains of each tetrad so closely appressed that the group is almost spherical. The individual cells are 21.1 to 29.6 μ in diameter. The exine is thin and flecked with small granules, and continuous from grain to grain over the whole tetrad, but the sutures between the adjoining grains are plainly visible through the exine. The intine is thick and hyaline, thicker on the walls of the dissepiments than on the outside walls. Each cell is provided with a single germinal area of thinner exine on its distal side and not sharply marked off from the rest of the exine.

The wood rush is common in woodlands almost throughout North America, also in Europe and Asia. It flowers very early in spring. Though wind pollinated its pollen is rarely caught on pollen slides, and does not cause hayfever.

Dicotyledons

The dicotyledons are the flowering plants which generally have obviously two seed leaves or cotyledons; occasionally, however, one or both may remain in the seed. The first foliage leaves are generally opposite. The stems are formed of bast, wood and pith, and may be increased in thickness by the annual addition of layers of wood and bast generated by a growing layer of cambium between them. The parts of the flower are seldom in threes, frequently in fours or fives.

The dicotyledons include about $\frac{5}{8}$ of the living flowering plants. Here belong all the angiospermous trees and shrubs, except such monocotyledons as some liliads, *Pandanales*, bamboos and palms. They can generally be distinguished by a cross section of their stem which shows the vascular tissue in an unbroken cylinder about the pith in the center or, if in separate bundles as in herbaceous or young woody stems, the bundles arranged in a ring.

Salicaceae (The Willows and Poplars)

The *Salicaceae* are trees or shrubs with simple alternate stipulate leaves, and dioecious flowers in catkins, appearing before or at the same time as the leaves, both male and female without perianth, borne in the axils of bracts.

The family comprises but two genera, the willows (*Salix*) and the poplars (*Populus*), mainly of the north temperate zone. The willows are primarily insect pollinated, but are certainly also wind pollinated to a certain extent. Their flowers which are borne in upright catkins (fig. 28), are conspicuously colored, sweet scented and provided with nectar which is secreted by a small scale at the base of each flower, and they succeed in attracting to themselves large numbers of bees. On the other hand the stamens protrude so that the pollen which is only slightly sticky is easily scattered in the air, and is often caught on atmospheric pollen slides several miles from the trees. The ability to secure pollination through the agency of either insects or wind probably explains the enormous latitudinal range and the variety of habitats occupied by the willows. The genus comprises 500 or more species ranging throughout north temperate and arctic regions. The arctic willow (*S. polaris*) reaches the extreme northern limit of vegetation; it has been found in flower and bearing seed on the northernmost tip of Greenland. Here the plants even when many years old have stems no thicker than the finger, which lie flat on the ground forming by their profuse branching a network through which the leaves and catkins peep out (THOROLD WULFF in RASMUSSEN 1916 Thule Expedition). A few species also occur in the West Indies and Central America and southward to Brazil and the Andes of Chile, and in the Old World southward to South Africa, Madagascar, Malay Peninsula, Java and Sumatra.

The poplars are entirely wind pollinated. Their flowers, borne in pendent catkins, are uncolored, without scent or nectar and unattractive to insects.

The willows and poplars are undoubtedly closely related though they may differ markedly in appearance. The leaves of the willows are mainly short stalked and linear, generally dark green above and whitened beneath, while those of the poplar are generally orbicular and long stalked, often with the stalk flattened laterally, at right angles to the blade, so that in a light breeze it is caused to twist into a vertical position as it gives before the air pressure, imparting to the leaves their characteristic trembling motion, whereas the leaves of the willow are lifted without twisting out of the horizontal. This is most beautifully expressed by TENNYSON in the lines:

Willows whiten, aspens quiver,
Little breezes dusk and shiver
Thro' the wave that runs forever
By the island in the river
Flowing down to Camelot.

Salix (The Willows)

The willows are trees or shrubs with scaly bark, slender tough branchlets often easily separating at the joints, simple, alternate leaves, generally lanceolate or linear, occasionally obovate or rotund, pinnately veined (fig. 29D).

The pollen grains (fig. 31B) of all species are essentially alike, spheroidal or oblatelly flattened, three lobed, ellipsoidal when dry, about 17.8μ in diameter, generally with three meridionally arranged furrows, exine reticulate with vertical edges which are thin and blade-like on their crests but thickened toward their bases. The reticulum is of coarser mesh toward the centers of the lunes, finer toward the poles and sharply bounded along the margins of the furrows with much smaller lacunae. The furrows are long and tapering, their membranes flecked as if covered with detached fragments of the exine, without a true germ pore but generally with a central bulge representing the germinal papilla. Willow pollen grains resemble somewhat those of the *Caprifoliaceae*, *Oleaceae* and *Sterculaceae*, but they may be distinguished from the first by their lack of a sharply defined germ pore, and from the two latter by their smaller size.

There are about 150 species of willow in North America. "The genus has long and justly been considered a difficult one to study. It is not that the genus is so large . . . or that the species are so variable in themselves, although a few of them are known to be very much so. The chief difficulty lies in the dioecious character of the plants, and the fact that in the majority of the species the flowers are produced before the leaves appear, or at least before they are large enough to become characteristic" (BALL 1900). Roughly speaking the willows are of two general types, those in which the catkins appear in advance of the leaves (the pussy willows) and those in which the catkins appear at the same time as the leaves. The pussy willows are mostly shrubs, and flower very early in spring, sometimes while snow is still on the ground, in the northeastern states as early as March. Those of the second group may be trees or shrubs or even, in the alpine and arctic species, almost herbaceous.

Among the pussy willows the European purple osier (*S. purpurea* L., fig. 28) is one of the most frequently cultivated for the beauty and luxuriance of its staminate catkins, the first heralds of spring so popular with children, and its long purple shoots which may be woven into baskets. It has become sparingly established in the Atlantic coast states, Ontario and Ohio. A wild native species commonly called pussy willow or silver willow (*S. discolor* Muhl.) is widely distributed in swamps and moist places throughout most of the northern United States and Canada, except far west. Among the tree forms the black or swamp willow (*S. nigra* Marsh.) is perhaps the largest and best known. It reaches a height of 120 feet with a trunk diameter of three feet, occurring along streams and on the shores of lakes and ponds throughout the United States and Canada, principally east of the Rocky Mountains. It is reported by WATRY and LAMSON (1931) as occurring in Needles, California, but unimportant in hayfever. The crack, brittle or snap willow (*S. fragilis* L.) having been introduced

into cultivation in America from Europe, has escaped and become thoroughly established in the Atlantic states and as far west as Kentucky. It is one of the commonest in villages and small towns. Both its English and Latin names refer to the fact that the twigs are easily detached from the main stem. As they fall they come down with the butt end first and often stick into the soft mud in an upright position and take root or, if they fall into the water, they may float away to establish new colonies wherever they become stranded. This characteristic is very convenient for the pollen collector; it is only necessary for him to shake a flowering tree vigorously, then pick up the fallen twigs with their yellow catkins. The white willow (*S. alba* L.) and the weeping willow (*S. babylonica* L.), two very beautiful



FIG. 28. — Willow flowers (*Salix purpurea*).

introduced species, the one from Europe the other from Asia, are much planted in parks and along streams.

Though each species of willow has a relatively short flowering period there are so many of them that the willow pollen season may extend for more than two months, starting in March and lasting until June, or even longer where some of the late-flowering species occur. Apparently no attempt has ever been made to distinguish between the different willows in hayfever studies; indeed any such distinction seems to be unnecessary. Though willow pollen is frequently caught in abundance on atmospheric pollen slides all available evidence seems to show that it is of only minor and incidental importance in hayfever.

For a further study of this interesting group the reader is referred to the works of BALL (1924 and pp. 128-139 in COULTER and NELSON, 1909) and SARGENT (1922).

Populus (The Poplars, Aspens and Cottonwoods)

The poplars are small or large trees, with pale smooth furrowed bark, light brittle wood, scaly resinous buds and long petioled leaves (fig. 29). They are dioecious with their flowers in long pendent drab colored catkins, opening before or at the same time as the leaves, generally very early in spring.

Their pollen grains (fig. 31C) are spheroidal or more or less deformed as if by pressure from each other within the anther, without pores or furrows, 27 to 34 μ in diameter. The exine is thin and fragmentary consisting of a network of granules spread loosely and thinly over the intine. The latter is thick and hyaline. These grains bear no obvious resemblance to those of the willows, since the characteristic exine of the latter is here a vanishing remnant. Still in the faint suggestion of its reticulate structure it seems to show family relationship with the willows. Wind pollination almost invariably leads to a reduction in the thickness of the exine with an attendant loss of its sculpturing, and a compensating increase in the thickness of the intine. The pollen grains of the poplars, as compared with those of the willows, are an outstanding example of this law.

In keeping with their mode of pollination exclusively by wind the flowers of the poplars are uncolored, unscented and not provided with nectar. They generally have more stamens than those of the willows and produce very much more pollen which is not at all sticky and is known to be carried great distances by the wind.

The genus comprises about 34 species of which about 15 are found in North America. They range from the Arctic circle to northern Mexico and Lower California and from the Atlantic to the Pacific, in the New World, and from the Arctic to northern Africa, the southern slopes of the Himalayas, central China and Japan, in the Old World. In the extreme north the poplars form great forests, and are common on alluvial bottom lands of streams and on high mountain slopes.

In cities several species, in America mostly introduced, are favorite trees for street planting. The white or silver poplar (*P. alba* L.) also called abele, is a European species commonly planted on streets and in yards. It is a large tree with broad leaves, dark green above and white and downy below. Its leaf petioles are not flattened, consequently its leaves do not have the trembling motion characteristic of most species. Another introduced species is the black poplar (*P. nigra* L.) native of Europe and Asia. Its characteristic form is round headed pyramidal, and of medium height, but it is exceedingly variable. Many of its varieties have been named; one of these is the tall graceful columnar form known as Lombardy poplar (var. *italica* DuRoi) extensively planted along city streets and as a wind break. Its leaves are small and triangular, smooth and green on both sides, the leaf stalks flattened. Also involved in street planting are a number of

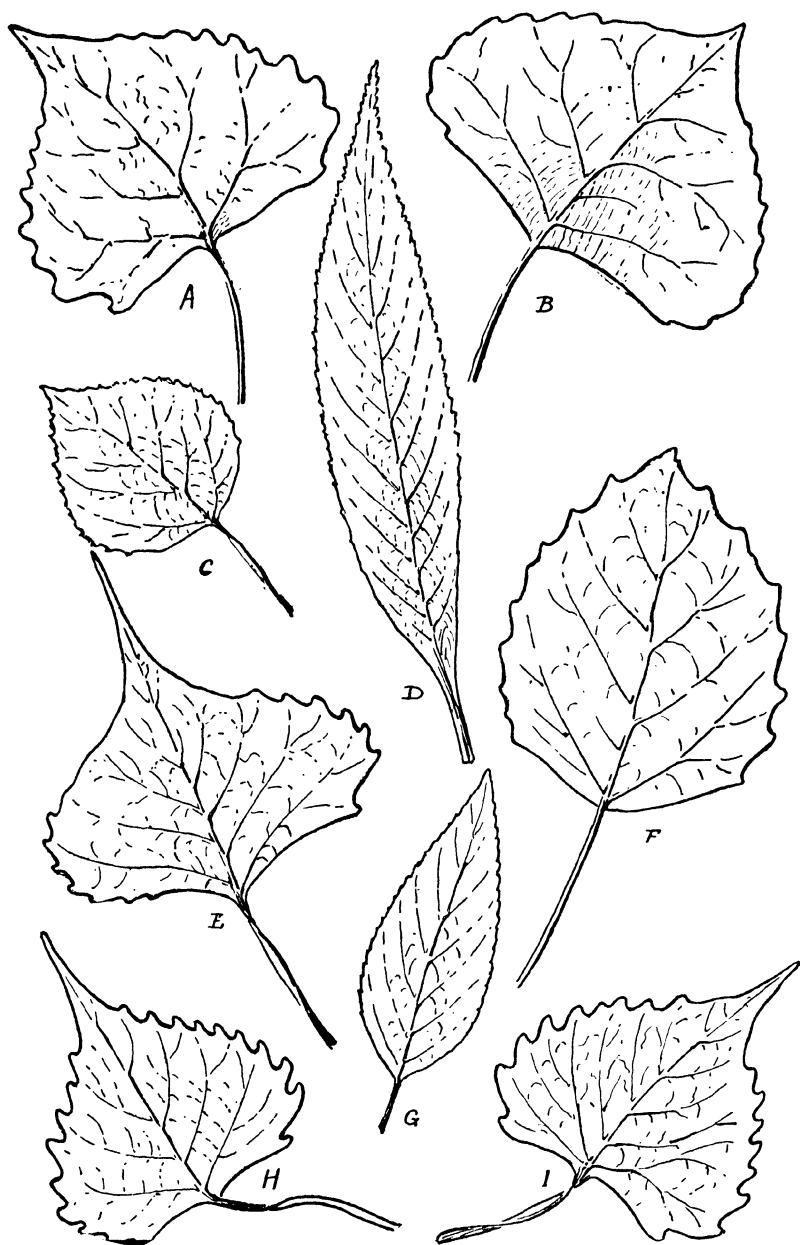


FIG. 29. — POPLAR AND WILLOW LEAVES: A, Valley cottonwood (*Populus Wislizenii*); B, California cottonwood (*P. Fremontii*); C, Quaking aspen (*P. tremuloides*); D, Crack willow (*Salix fragilis*); E, Western cottonwood (*P. Sargentii*); F, Large-toothed aspen (*P. grandidentata*); G, Willow-leaved or Mountain cottonwood (*P. angustifolia*); H, Cottonwood (*P. texana*); I, Cottonwood (*P. Fremontii*).

hybrids between *P. nigra* and *P. balsamifera* (REHDER 1940). These are generally known as Carolina poplars or *P. canadensis* Moench among horticulturists, though the group can not be regarded as a botanical species; it is rather a collection of hybrids. Most of them occur only in the staminate form and are always propagated vegetatively so that every tree of each variety is really a part of the original hybrid, horticulturally spoken of as a clone. One of the best known of these is the Eugene poplar, known to horticulturists as *P. canadensis Eugèni* Schelle or as *P. Eugenei* Simon-Louis, which originated near Metz, Lorraine.

There are also many native species which must be considered in hayfever studies. Even when these do not grow near dwellings they may be effective in causing hayfever on account of the buoyant nature of their pollen. One of the commonest and most widely distributed is the quaking or trembling aspen (*P. tremuloides* Michx.) also called American aspen or quiver-leaf. It is a small graceful tree scarcely exceeding 40 feet in height, with small leaves green on both sides and with finely serrate margins, their petioles very much flattened. It is found on the borders of streams, lakes and in meadows almost throughout Canada from Newfoundland to Alaska and southward to New Jersey, Kentucky, Nebraska and California, and in the Rocky Mountains following the Canadian zone even into Mexico. Its flowering period, generally of only a few days duration in any locality, occurs between March and May, depending upon the climatic factors of the locality. Another poplar of wide distribution is the tacamahac, balsam or Carolina poplar (*P. tacamahaca* Mill.). It is a tall tree with leaves green on both sides and with round petioles. It ranges from Newfoundland to Alaska wherever trees can grow, and southward as far as Oregon and New York. It flowers in April. This species is sometimes known as *P. balsamifera* DuRoi and as a consequence confused with *P. balsamifera* L. which is quite different. It occurs in several varieties. The balm of gilead (*P. tacamahaca candicans* Gray, *P. candicans* Ait.), known only in the pistillate form, is often considered one of them (SARGENT 1922).

In the northeastern states are two other common species, one the large-toothed aspen (*P. grandidentata* Michx.) easily recognized by its coarsely toothed leaves, which are green on both sides and with flattened petioles. It has a range from Nova Scotia to Minnesota and southward to Tennessee. The other, often associated with it, is the cottonwood (*P. balsamifera* L., *P. angulata* Michx. f.) a large tree with massive spreading branches, with deeply furrowed gray or brown bark. The species ranges from Vermont to Mississippi but is not common. However several varieties occur; one of these *P. balsamifera virginiana* Sarg. (*P. virginiana* Fougèroux, *P. deltoidea* Marsh) is the common cottonwood of the East, generally going by the name of *P. deltoides*, necklace poplar. Two other varieties, var. *pilosa* Sarg. and var. *missouriensis* Rehd. occur in the South.

In the Rocky Mountains are found still others. The western or river cottonwood (*P. Sargentii* Dode) is similar to the necklace poplar; it is even regarded by some as a variety of it (*P. deltoides occidentalis* Rydb.). It is the principal tree in the eastern foothills of the Rocky Mountains, ranging

through the mountainous sections from Saskatchewan to New Mexico and eastward to the Dakotas, Nebraska and Kansas. It flowers in March and April and is probably the cause of some hayfever. On the western slope of the Rocky Mountains is found the willow-leaf cottonwood (*P. angustifolia* James) also known as black, mountain or narrow-leaved cottonwood. It is the common cottonwood of the Rocky Mountain region reaching from western North Dakota, southern Saskatchewan and eastern Washington southward to northern New Mexico and Arizona. It flowers in April and May and seems to be the cause of some hayfever. Rydberg's or smooth-barked cottonwood (*P. acuminata* Rydb.) is a similar tree but with leaves rhombic lanceolate to ovate. It is found on the banks of streams throughout the Rocky Mountain region from Saskatchewan to western Texas and to eastern Utah and Montana. It is sometimes planted as a street tree. The valley cottonwood (*P. Wislizenii* Sarg.) is a large tree with spreading branches and deltoid coarsely toothed leaves. It occurs in western Texas, New Mexico and part of Colorado, and is perhaps the most familiar tree in New Mexico. It is especially common in the flood plains of the Rio Grande and San Juan River, and is the most commonly planted shade tree of the cities. It flowers in March and April and is believed to be an important cause of hayfever.

In the far west are two other species, the California cottonwood and the Arizona cottonwood, which are believed to cause some hayfever. California cottonwood (*P. Fremontii* Wats.) also known as Fremont's cottonwood, is a tall tree reaching 100 feet in height and with trunk diameter of five to six feet, with broad coarsely toothed leaves, green on both sides and with flattened petioles. It is found on the Pacific coast of California and part of Lower California and especially in the San Joaquin valley, and is often planted as a shade tree in southern California. It flowers in February and March and is believed to be an important cause of hayfever. Arizona cottonwood (*P. McDougallii* Rose), the cottonwood of the Colorado River delta, is similar and closely related; in fact it is sometimes regarded as merely a variety. It is found near springs and on the banks of streams from San Bernardino County, Nevada, to Yuma, Arizona, where it is probably the only cottonwood occurring naturally. It is also planted as a street tree in the towns of southern California.

Betulaceae (The Family of the Birches, Alders, Ironwood and Bluebeech)

The *Betulaceae* are trees or shrubs with slender branchlets marked by numerous pale lenticels; their leaves pinnately veined, doubly serrate, deciduous; their flowers monoecious in pendent catkins, opening in spring either before or at the same time as the leaves. Their pollen grains are smooth or faintly granular, spheroidal or oblately flattened, 20 to 40 μ in diameter, provided with 3 to 7 germ pores which tend to be equally spaced around the equator, generally somewhat protruding and giving the grain an angular outline.

The family comprises six genera confined to the northern hemisphere; five are native of North America. All species are wind pollinated and shed exceedingly large

amounts of pollen. The birches themselves are known to occasionally cause severe hayfever, but it is not known what part the other members of the family play. In view of the close relationship existing between the several genera, however, it is to be expected that sensitization to the pollen of the birches would generally imply sensitization to that of the other members of the family.

Betula (The Birches)

The birches are trees with smooth tough resinous bark marked by numerous horizontal lenticels serving as breathing pores. In the younger trees the bark generally has a tendency to separate in papery layers but may become deeply furrowed and scaly at the base of old trunks. The pistillate catkins persist throughout most of the winter as conspicuous brownish cones with slowly deciduous scales, discharging their small winged seeds which are blown about the surface of the snow. The staminate flowers are borne in long pendulous catkins (fig. 30) which fall off as soon as they shed their pollen.

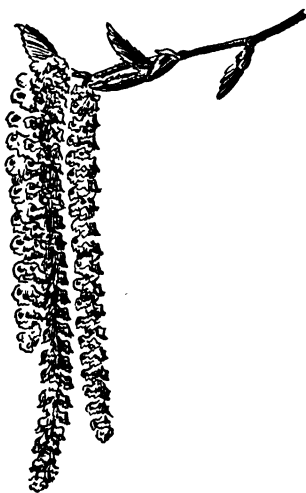


FIG. 30. — White birch flowers (*Betula alba*).

The pollen grains (fig. 31D) are flattened angular, 20 to 40 μ in diameter (less than 30 μ in American species); with three pores, or occasionally some grains with four and higher numbers up to 7, equatorially arranged, strongly aspidate and protruding, imparting to the grain its angular appearance, their apertures broadly elliptical and meridionally oriented or, if there are more than three pores, biconvergent. The exine is nearly smooth or slightly granular. Birch pollen grains are scarcely distinguishable from those of *Carpinus*. In fact it is only with difficulty that they can be distinguished from those of most members of the *Betulaceae* and *Myricaceae*. For a detailed discussion of this problem the reader is referred to "Pollen Grains" (WODEHOUSE 1935).

The birches flower early in spring, generally just before or at the time of the unfolding of the leaves, in the northeastern United States and Canada

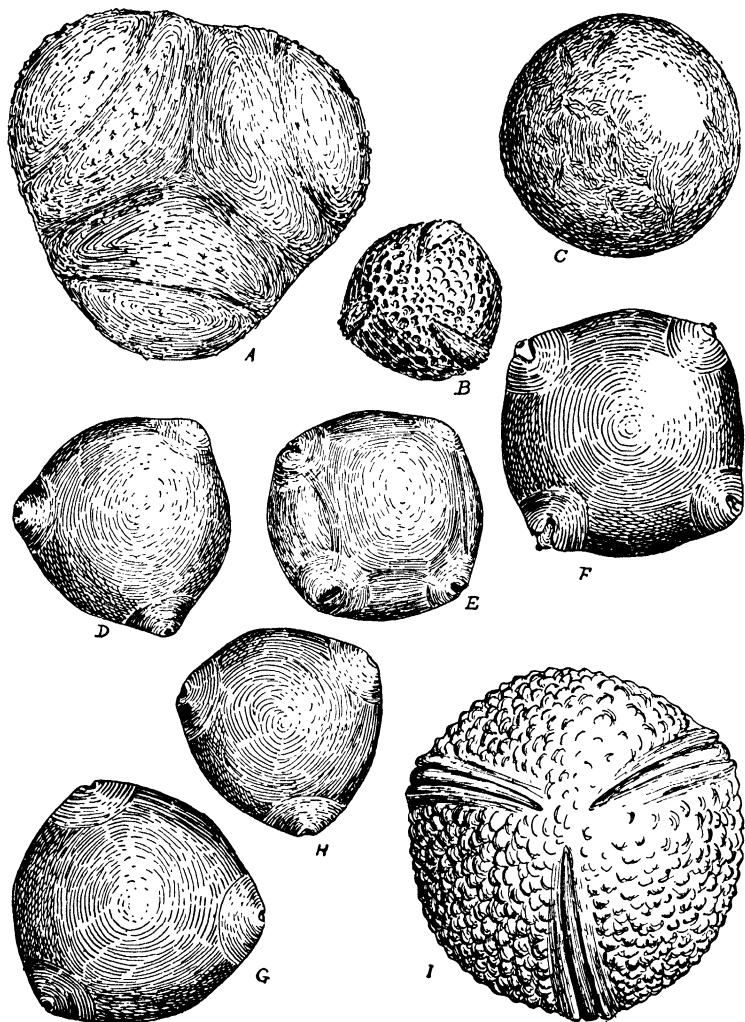


FIG. 31.— POLLEN GRAINS OF RUSH, WILLOW, BIRCH AND BEECH FAMILIES: A, Rush (*Juncus*); B, Willow (*Salix*); C, Poplar (*Populus*); D, Birch (*Betula*); E, Alder (*Alnus*); F, Bluebeech (*Carpinus*); G, Ironwood (*Ostrya*); H, Hazel (*Corylus*); I, Beech (*Fagus*). All magnified 1300 times.

late April or early May, thus following by several weeks the poplars, hazels, pussy willows and elms. They shed large quantities of pollen which is known to be among the most important tree pollens in hayfever. The

flowering period of each species is short, generally less than a week, but those of the different species do not coincide so the birch hayfever season may last several weeks, or about a month where several species are involved; they appear to be about equally effective in causing hayfever and allergenically indistinguishable.

In the northern United States three species, the gray or white birch, the yellow or gray birch and the cherry or black birch, are often found growing together. They flower in succession, beginning in April or May with the gray birch and ending several weeks later with the black birch. The gray or white birch (*B. populifolia* Marsh.), sometimes called the American white birch, is only a small weak tree and short lived, but graceful and beautiful, characteristic of dry gravelly barren soil and depleted farm lands from Nova Scotia to Delaware and westward to Wisconsin, Minnesota and western Ontario. Its bark tends to separate in papery layers, but sheets large enough to be of any practical use can not be obtained. The black or cherry birch (*B. lenta* L.) is a large forest tree reaching 80 feet with dark brown almost black bark with no tendency to separate in layers but which gives the trunk a decided resemblance to that of a cherry tree. Its twigs and leaves have a pleasant wintergreen odor; in fact an oil which is distilled from the twigs is the 'oil of wintergreen' of commerce. This species has a more southerly distribution from New England to Florida and westward to Minnesota. The yellow or gray birch (*B. lutea* Michx.) is also a large forest tree, reaching a height of 100 feet with a trunk diameter of four. Its bark is yellowish or grayish and separates in lustrous layers no thicker than tissue paper which may often be seen decorating the trunks of old trees with rows of silvery curls, particularly the trees which are found deep in the forest where they are protected from winds. This species has a more northerly distribution, from Pennsylvania and Connecticut to Newfoundland, and westward to Manitoba.

In the South occurs the red birch (*B. nigra* L.), also known as river or water birch. It is a tall tree reaching 100 feet in height. On young trees and large branches the bark is of a silvery or brownish lustre and separates freely into thin papery scales, but on old trees the bark is dark reddish brown and deeply furrowed. It is the common birch of the southern states where it is found on the banks of streams, ponds and swamps, in deep rich soil, from Connecticut to Florida and westward to Minnesota and Texas.

The common birch of Canada is the paper or canoe birch (*B. papyrifera* Marsh.) a tall and valuable forest tree, extending almost throughout Canada and southward to Pennsylvania, Michigan, Nebraska, Wyoming and Montana and, in its several varieties, reaching to Washington. Its white bark which may be stripped in a single piece from the whole trunk has furnished the northern tribes of aboriginal Americans their canoes and many utensils, and its wood, though light and soft, has many uses.

The cultivated birches are principally varieties of the Asiatic and European *B. pendula* Roth or *B. alba* L. The latter flowers a week or more earlier than the native birches in the northeastern United States.

***Alnus* (The Alders)**

The alders are shrubs or trees with broad, toothed leaves, pinnately veined, and alternately arranged on their branches. The flowers of both sexes are borne in catkins (fig. 32), the staminate pendulous and early deciduous, the pistillate more or less erect with woody scales and persistent, expanding very early in spring before the leaves, or toward the end of summer.

Their pollen grains (fig. 31E) are oblatelly flattened, angular, 19 to 27 μ in diameter, with 4 or 5, rarely 3 or 6 germ pores which are aspidate, with markedly thickened rim and protruding, their apertures narrowly elliptical or slit shaped. The texture of the exine is smooth or slightly granular. A striking character of these grains is their possession of band-like thickenings of the exine extending in broad sweeping curves from pore

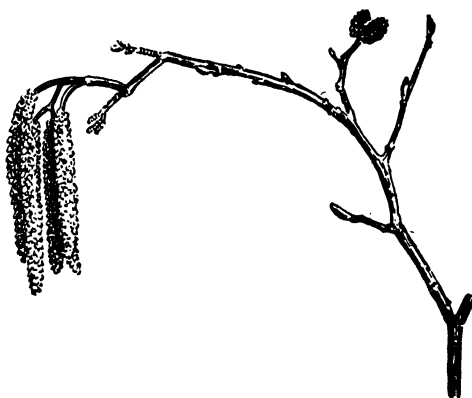


FIG. 32.— Alder flowers (*Alnus*).

to pore in pairs, one on either side of the equator. These serve to distinguish alder pollen grains from all others of the same general character.

Nine species are native of North America, and the European black alder (*A. vulgaris* Hill) is sometimes cultivated, and has become naturalized locally in the northeastern states. Of the native species the speckled or hoary alder (*A. incana* Moench) is a shrub 8 to 40 feet high, widely distributed from Newfoundland to Saskatchewan and southward to Nebraska, Ohio and Pennsylvania. Smooth or tag alder (*A. rugosa* Spreng.) is a shrub of similar appearance but has a more southerly distribution, from Maine to Florida and westward to Texas, Nebraska and Minnesota. It flowers very early, in March or April, even in January and February in the southern part of its range, among the very first flowers of spring. In the western part of the country are two alders large enough to properly be regarded as trees. The Sitka or wavy-leaved alder (*A. sinuata* Rydb.) is a small tree attaining a height of 45 feet common along mountain streams and lakes where it often forms dense thickets in the Canadian and Hudson Zones

from Alaska to Oregon and eastward to Saskatchewan and Colorado. It flowers late, the flowers appearing with or after the leaves from May to July. The white alder (*A. rhombifolia* Nutt.) is a small tree, sometimes reaching a height of 75 feet, the common alder of the valleys of central California. It ranges from northern Lower California to southern British Columbia and eastward to the western slope of the Rocky Mountains in Idaho. It flowers in winter or early spring, generally December or January.

Carpinus (Hornbeam or Ironwood)

The hornbeams are trees or shrubs with smooth gray bark, and furrowed or ridged stems. The flowers (fig. 33) open before the leaves, in



FIG. 33.— American hornbeam staminate and pistillate catkins (*Carpinus caroliniana*).

April or May, the staminate in short pendent catkins, the pistillate in short terminal spikelets. Each flower is subtended by a flattened bract which enlarges at maturity to resemble a three pointed leaf. The pollen grains (fig. 31F) are similar to those of birch but more nearly circular in outline when seen in polar view, about 26.5μ in diameter, though there is some variation in their size. They have three or four pores, in the American hornbeam generally three, in the European generally four. The pores are small, nearly circular and capped by a small operculum. Their rims are scarcely thickened yet the pores bulge prominently. The exine is smooth except around the pores where it may be slightly granular.

The genus comprises about 15 species distributed almost throughout the northern hemisphere. The American hornbeam or bluebeech (*C. caro-*

liniana L.), the only species native of North America, is a small tree common in the eastern United States in moist woods and along streams from Nova Scotia to Minnesota and southward to Florida and Texas. It flowers just before the birches and its pollen is frequently caught on pollen slides. The European hornbeam (*C. Betula* L.) is a fair sized tree, reaching 70 feet and is commonly planted in North America. The pollen of both species reacts cutaneously with hayfever patients and appears to be a complicating factor in cases of birch hayfever.

Ostrya (Hop-hornbeam, Ironwood)

The ironwoods (fig. 34) are small trees with scaly bark, with terminal



FIG. 34. — Hop-hornbeam (*Ostrya virginiana*).

pistillate catkins, their flowers in pairs subtended by a persistent bractlet which enlarges into a bladder-like sac, making the catkins look like hops at maturity.

The pollen grains (fig. 31G) are similar to those of birch, about 27.5μ in diameter, slightly flattened oblatelly and somewhat angular in outline, with generally three pores, rarely four, their apertures nearly circular and their membranes flecked with granules which tend to be aggregated toward the center, not forming a sharply defined operculum as in the grains of *Carpinus*. The exine is decidedly granular throughout, and the subexineous thickenings underlying the pores are very much smaller than in the grains of *Carpinus*.

The genus comprises four species, two of them native of North America. The hop-hornbeam (*O. virginiana* Willd.), also called ironwood, hardhack or leverwood, is generally a small tree but may reach a height of 50 or 60 feet. It is common and widely distributed from Cape Breton Island to Manitoba and southward to Florida and Texas. It flowers in April or May shedding large amounts of pollen.

Corylus (Hazels or Filberts)

The hazels are shrubs or small trees. Their staminate flowers are borne in long pendent catkins (fig. 35), their pistillate flowers few in clusters at the ends of branches, maturing to form large nuts wrapped in their involucre of leaf-like bracts which may be distinct, or united into a tubular beak.

The pollen grains (fig. 31H) are similar to those of the birches but their pores, which are always three, less raised and their apertures nearly or quite circular.

The genus comprises 7 species of Europe and North America. The European species, (*C. Avellana* L.), the common hazelnut or filbert, is the one most frequently planted in America. It occurs in many varieties which are cultivated for their fruits or for ornaments. Three species are native of

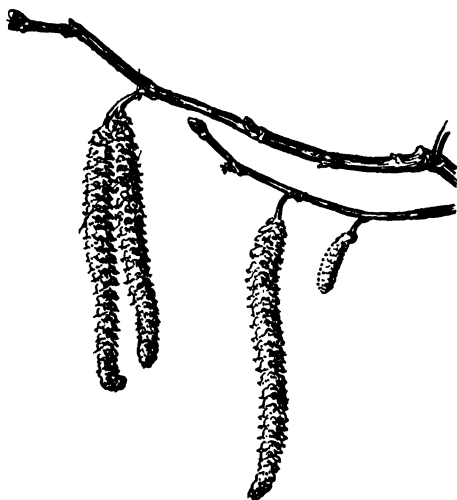


FIG. 35. — Hazel flowers (*Corylus*).

North America. In the eastern states the American hazel (*C. americana* Walt.) and the beaked hazel (*C. rostrata* Ait.) often grow together in thickets and along roadsides. Both are small shrubs, so similar to each other that it is difficult to tell them apart when they are not in leaf. The leaves of the beaked hazel, however, may be distinguished by their incised and serrate margins from those of the American hazel which are merely serrate. In their fruits the distinction is more marked; that of the American hazel is enclosed in two broad lacinate bracts giving it something the appearance of an old fashioned bonnet, from which it is called the bonneted hazelnut or filbert. The involucre bracts of the beaked hazelnut are united and prolonged into a tubular bristly beak to which both its English and Latin

names refer. Both species flower very early in spring. All winter long the staminate catkins of the hazels may be seen hanging stiffly from the young branches, but at the first suggestion of spring they lose their stiffness, open their flowers and shed their pollen, which is copious enough to be caught on pollen slides, and is among the first to make its appearance, usually together with the first few grains of pine and juniper pollen. In the East these two species have much the same distribution; the American hazel extends from Maine to Florida and westward to Montana and Wyoming, while the beaked hazel extends from Nova Scotia to Georgia and westward to Oregon and British Columbia. On the Pacific coast in the moist canyons of the Transition Zone from British Columbia to California is found the California hazel (*C. californica* Rose) similar to the beaked hazel both in the double toothed character of its leaves and its beaked fruits. In fact it is frequently regarded as a variety and designated as *C. rostrata californica* A. DC.

Fagaceae (The Beeches, Oaks, Chestnuts and Chinquapins)

The beech family includes six genera and about 400 species of trees and shrubs of wide distribution but mainly confined to the northern hemisphere. The five genera, *Fagus*, the beeches; *Quercus*, the oaks; *Castanea*, the chestnuts; *Castanopsis*, the chinquapins; and *Lithocarpus*, the tan-bark oaks, are represented in America; the sixth genus, *Nothofagus*, is established to receive the beeches of the southern hemisphere. All are monoecious, the staminate flowers borne in unisexual heads or in erect or pendent catkins, usually appearing in late spring or early summer, at about the same time that the leaves unfold, or shortly after. The beeches and oaks are entirely wind pollinated and are characterized, especially the latter, by the enormous quantities of pollen they shed. The chestnuts, chinquapins and tan-bark oaks are primarily insect pollinated. Their staminate catkins are stiff and more or less erect, never pendent as in the oaks and most other wind pollinated forms, they produce much less pollen than the oaks and beeches, and are characterized by a strong disagreeable odor, and succeed in attracting to themselves many honey-gathering insects.

The pollen grains of the oaks (fig. 40A) and beeches (fig. 31I) are similar to each other, being of medium size and provided with a rather thin and warty-granular exine. But they bear no resemblance to those of the chestnuts and chinquapins which are very small and provided with a perfectly smooth exine. The difference between these two types of grain is far greater than should be expected between plants closely enough related to belong to the same family, and appear to be the result of adaptations to their respective modes of pollination.

Fagus (The Beeches)

The beeches are trees with smooth light-gray bark, and yellowish-green staminate flowers in heads, opening at the same time as the leaves. The pollen is buoyant and easily dispersed by the wind, and is frequently caught

on pollen slides, but is generally much less abundant than that of oaks. The grains (fig. 31I) are approximately spherical, about 40μ in diameter with three long tapering furrows meridionally arranged, their margins slightly raised, their membranes smooth and provided with a small elliptical germ pore. Underlying each pore within the cell is a small globular hyaline body.

The genus comprises four species of the northern hemisphere. Only one, the American beech (*F. grandifolia* Ehrh.), however, is native of North America, ranging from Nova Scotia to Florida and westward to Missouri and Texas. Two others occur in eastern Asia and one in Europe. This latter (*F. sylvatica* L.) is the species generally cultivated in the United States. It occurs in several varieties of widely different appearance, the commonest of which are those having pendulous branches, pyramidal habit, leaves purple or deeply cut. The European species appears to shed very much more pollen than the native American species, but neither appears to be more than a minor contributory factor in hayfever.



FIG. 36. — White oak (*Quercus alba*), flowering twig.

Quercus (The Oaks)

The oaks are noble deciduous or evergreen trees, rarely shrubs. Their staminate flowers are borne in slender pendulous catkins (fig. 36), with usually six-parted calyx and 4 to 12 stamens, opening at the same time as or just after the unfolding of the leaves, generally in May. The oaks shed enormous quantities of pollen, outranking that of all other plants in regions where the trees are abundant. Oak pollen has to its credit rather more hayfever cases than most trees but the number is in no way commensurate with the amount of pollen they shed.

Oak pollen grains (fig. 40A) are spheroidal or oblately flattened and triangular in outline, tricolpate or, occasionally, some grains with supernumerary furrows, the latter arranged according to the trischistoclastic system, long and tapering to pointed ends, their margins not raised, their membranes smooth and provided with a small pore, but the furrow membranes are invariably ruptured when the grains are prepared for microscopic examination unless special precautions are taken to prevent its occurrence. Underlying the center of each furrow, within the body of the cell, is a wedge-shaped hyaline body centripetally oriented. The exine is rather thin but coarsely warty-granular and the intine thick.

The genus comprises about 275 species of the northern hemisphere, extending into the tropics in mountainous districts. About 65 are native of North America, and a few European species as the English oak (*Q. Robur* L.), the cork oak (*Q. suber* L.), and *Q. sessiliflora* Salisb. are cultivated to a limited extent in the eastern states.

Taxonomically the oaks are exceedingly difficult. This is partly because many species are variable and exhibit a strong tendency to form natural hybrids, and often the differences between species are very slight. However this fact probably makes it unnecessary for hayfever students to distinguish them precisely. For example, BROWN (1932) states "There are at least twenty different species growing in the Middle Atlantic States but they are all so closely related that an oak pollen mixture is sufficient for routine testing". The English names are often used to designate groups of species which are related or similar rather than individual species, a procedure which though not strictly scientific is eminently practical. According to their natural relationships the genus may be roughly divided into four groups, the Black Oaks, Willow Oaks, White Oaks and Chestnut Oaks. Besides these groups which are based on actual relationship other English group-names bring together those which are similar though not necessarily closely related. Thus the Live Oaks are those which retain their leaves throughout the winter—these include some of the willow oaks and white oaks. The Scrub Oaks are those which do not grow into tall trees and often form dense thickets. These are mostly red or white oaks.

The Black Oaks:—These are distinguished by having their leaves deeply lobed and the lobes pointed and tipped with a bristle (fig. 37A). Their fruit matures at the end of the second season and the cup of the acorn is silky inside. Their minute greenish flowers have 4 to 6 stamens. Perhaps most representative of the Black Oak group is the black oak itself (*Q. velutina* Lam.) and the red oak (*Q. rubra* L., fig. 37B). At any rate these are the best known and the most widely distributed members of the group in the eastern United States. They have nearly the same range, both extending from Maine to Florida, and westward to Minnesota and Kansas, with the red oak reaching northward into Nova Scotia and the black westward into Texas. Other common species of this group are the gray or red oak (*Q. borealis* Michx. f.) extending from Nova Scotia to Florida and westward to Kansas, the scarlet oak (*Q. coccinia* Wang.) also known as Spanish, black

or red oak, with a distribution from Maine to North Carolina and westward to Ontario and Missouri, and the Spanish, swamp or pin oak (*Q. palustris*)

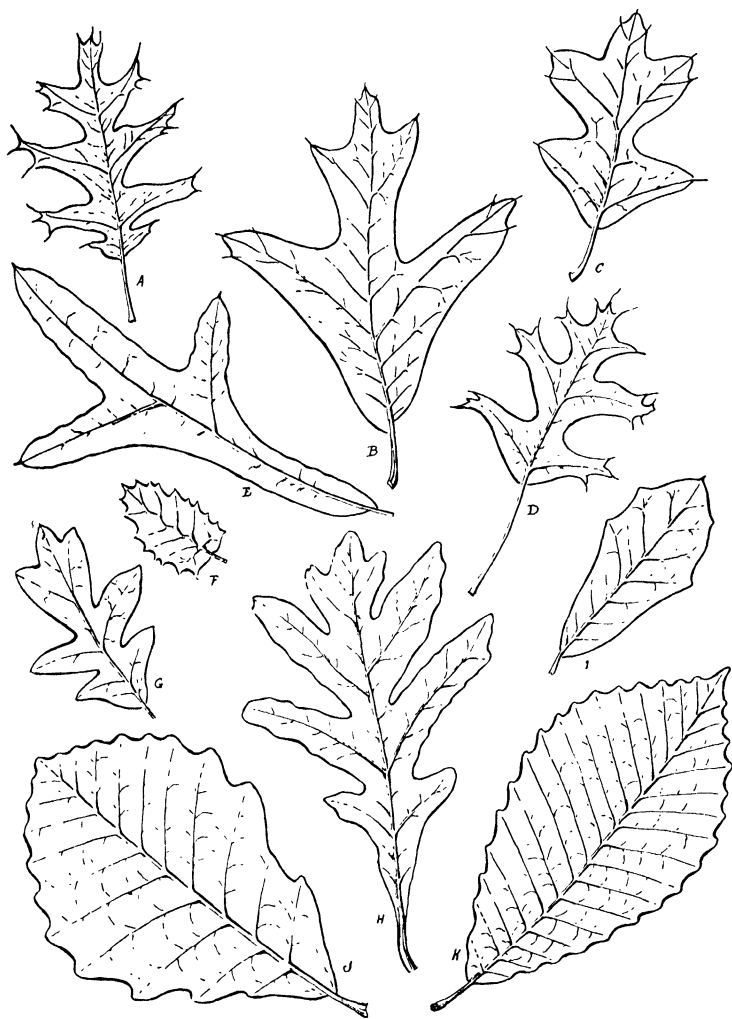


FIG. 37. — OAK LEAVES: A, Black oak (*Quercus velutina*); B, Red oak (*Q. rubra*); C, Scrub oak (*Q. ilicifolia*); D, Spanish oak (*Q. palustris*); E, Willow oak (*Q. phellos*); F, Coast live oak (*Q. agrifolia*); G, Scrub oak (*Q. venustula*); H, White oak (*Q. alba*); I, Live oak (*Q. virginiana*); J, Swamp white oak (*Q. bicolor*); K, Chestnut oak (*Q. prinus*).

DuRoi, fig. 37D) which is generally a smaller tree with slender drooping branches. It has a more restricted range, reaching only from Massachusetts to Virginia and westward to Michigan and Arkansas.

Also belonging to this group are the two species known as black-jack oak (*Q. marilandica* Muench. and *Q. nigra* L.). The former is also called barren oak and is characteristic of dry sandy or clay barrens, from Long Island and Staten Island southward to Florida and westward to Nebraska and Texas. The latter is also called water, pin, spotted, duck, or 'possum' oak and is characteristic of high sandy borders of swamps and streams and rich bottom lands throughout the southeastern states from Delaware to Florida and westward to Missouri and eastern Texas. It is commonly planted as a shade tree in the streets and squares of southern cities.

The Willow Oaks are similar to the black oaks, except that the leaves are not generally lobed (fig. 37E); instead they are lanceolate, ovate or oblong and with their margins entire or merely toothed. The group is small and could quite properly be regarded as a subdivision of the Black Oaks. The most representative species is, perhaps, the willow oak (*Q. Phellos* L., fig. 37E), a large tree characteristic of the coastal plane and adjoining territory, in swamps and on banks of streams and sandy bottoms from southern New York to Florida and westward to Texas and Missouri. Also belonging to this group are the western live oaks which will be discussed later.

The White Oaks comprise some of our largest and handsomest members of the genus. They may generally be easily distinguished from those of the previous groups because their leaves are lobed (fig. 37H) and the lobes rounded and not bristle tipped. The fruit matures at the end of the first season, and the cup of the acorn is quite smooth inside. The bark is generally flaky and light in color. The most representative species is the white oak (*Q. alba* L.), a large forest tree reaching 100 feet in height and with a broad spreading crown of thick heavy branches. It is one of the most abundant species throughout the eastern states from Ontario to Florida and westward to Minnesota and eastern Texas. Others of this group are the post or iron oak (*Q. stellata* Wang.) characteristic of dry sterile and acid soils such as Cape Cod and the islands of southern Massachusetts southward to Florida and westward to Iowa, western white oak (*Q. Garryana* Dougl.) also called Garry's or Oregon oak, of the Pacific coast where it is rather rare and local, confined to valleys and dry gravelly slopes from Vancouver Island southward to Oregon and northern California, but it has the distinction of being the only oak in British Columbia. Also of the Pacific coast is the evergreen, mesa or Engelmann's oak (*Q. Engelmannii* Greene). The leaves of this are persistent throughout the winter but fall with the appearance of the new leaves in spring. It is confined to the mountains of southern California.

The Chestnut Oaks, except that the leaves are sinuately toothed rather than lobed, are similar to the White Oaks. The most representative species is that of the chestnut oak (*Q. Prinus* Engelm.) with leaves elongate coarsely toothed and closely resembling those of the chestnut (fig. 37K). It is a large tree, with thick and deeply furrowed bark, characteristic of rocky banks and hillsides from Maine to Alabama and westward to Tennessee.

Also belonging to this group is the swamp white oak (*Q. bicolor* Willd.) which closely resembles the white oak, having leaves more nearly pinnatifid (fig. 37J) than toothed and with similar whitish flaking bark. It is a large and stately tree of less spreading habit than the white oak, on borders of streams and swamps from Quebec to Georgia and westward to Minnesota and Arkansas.

Live Oaks: — Regardless of their botanical group, many of the evergreen oaks are called Live Oaks. Usually their leaves are thick and leathery and very stiff and more or less evergreen. Three of these are western. The coast live oak or encina (*Q. agrifolia* Née) is a large and beautiful spreading tree with leathery prickly-tipped leaves (fig. 37F) falling during winter and early spring, native of the coastal regions of California. The interior or highland live oak (*Q. wislizenii* A. DC.) is somewhat similar but with leaves deciduous during their second summer and autumn, native of the interior of California. The maul oak (*Q. chrysolepis* Liebm.) is similar but of wider distribution in Oregon and California and with leaves falling mostly not before their third or fourth year. All three of these are regarded botanically as Willow Oaks. In common parlance, however, they are the live oaks so characteristic of the landscapes of California. Three other species of live oak belong to the southeastern area of the United States. Only one, the eastern or Texas live oak (*Q. virginiana* Mill.), is a large tree, botanically a white oak. It is found principally near the coast from Virginia to Florida and westward to Texas and Mexico. Its leaves (fig. 37J) fall in the spring with the appearance of the new set. The other two eastern live oaks, the dwarf live oak or scrub live oak (*Q. minima* Small) and the twin live oak or scrub oak (*Q. geminata* Small), are characteristic of the coastal plain region of the southeastern states. Botanically they are white oaks and so closely related to *Q. virginiana* that they are sometimes regarded as varieties of it.

Scrub Oaks: — The oaks which do not grow into large trees but, instead, tend to form thickets, are called scrub oaks or shrub oaks. Generally speaking, in the east the scrub oak is *Q. ilicifolia* Wang., also called bear or black oak. It is occasionally a small tree but more often a shrub forming dense thickets in barren, sandy or rocky soil, from Maine to North Carolina and westward to Kentucky and Ohio. Its leaves (fig. 37C) have short triangular bristle-tipped lobes and it possesses other characteristics which assign it to the group of black oaks. In the Rocky Mountain states are found two other scrub oaks, *Q. venustula* Greene (fig. 37G) of limited distribution in the Sonoran Zone of southern Colorado and northern New Mexico, and *Q. Gunnisonii* Rydb. of Submountain Zones of Colorado, New Mexico, Arizona and Utah. Both of these are, botanically, white oaks. The California scrub oak is *Q. dumosa* Nutt., found throughout most of California and northern Lower California. It is evergreen, its leaves falling in spring with the appearance of the new set, so it could quite properly be regarded as a live oak, but it is not spoken of as such in California for it is

only a low shrub lacking the dignity and beauty there associated with the live oak. Botanically, it is, like its two eastern relatives, a white oak.

From this brief discussion many important species have had to be omitted. The student who wishes to go more thoroughly into the study of our native oaks will find them fully discussed in SARGENT'S Manual of the Trees of North America.

Casuarinaceae (The Australian Pines or Joint-firs)

The *Casuarina* family includes but a single genus of 25 species, of uncertain relationships. They are trees or shrubs with reduced leaves and jointed branches, giving them outwardly the appearance of primitiveness, but these are really characters achieved by reduction. The branchlets are green and function as leaves, resembling in appearance those of pine trees. Their true leaves are reduced to scales closely appressed in whorls around the nodes of the branchlets.

The resemblance of these plants to the pines is quite remarkable, but it is only superficial. They are truly angiosperms and their morphological characters, especially the course of the pollen tube in entering the ovule at time of fertilization, indicate that they are most probably related to the walnut family.

The *Casuarinas* are native of the Mascarene Islands, through Malaya to New Caledonia and Australia. Several species have been introduced into central and southern Florida where they are used as shade trees, windbreaks and sand binders. They are also often used as ornamentals and clipped as hedges.

The *Casuarinas* are wind pollinated and are reported to cause some hay-fever (ZIVITZ 1942).

C. equisetifolia Forst., Beefwood or Forestoak is perhaps the species most commonly planted as a windbreak and ornamental. It is noted for its rapid growth and is said to be capable of reaching a height of sixty feet in six years. It flowers sporadically almost throughout the summer and is particularly abundant in the neighborhood of Miami.

C. Cunninghamia is the common species of the west coast of Florida. It is particularly abundant in and around Tampa. It pollinates in late summer when its flowers form conspicuous reddish brown masses at the tips of its branches.

The pollen grains of the *Casuarinas* closely resemble those of the birch family and even more so those of some Asiatic species of the walnut family, which is strong evidence of their relationship with that group.

Juglandaceae (The Walnut Family)

The walnut family includes six or seven genera and about 35 species of tall trees with deciduous pinnate leaves, and monoecious flowers opening after the unfolding of the leaves. The fruit is a nut enclosed in a fleshy or woody shell which opens either by four valves or not of itself at all.

Only the walnuts (*Juglans*) and the hickories (*Carya*) occur in North America. All are wind pollinated and are noted for the large amounts of pollen that they shed, generally in May or early June, but their flowering periods are relatively short, and their pollen grains rather large, especially of the hickories, and not adapted to long range dispersal. Probably on account of this they claim only a small number of hayfever cases; only the California black walnut and pecan appear to be of much importance in hayfever.

Juglans (The Walnuts)

The walnuts are tall trees with furrowed scaly bark, and large deciduous leaves with many leaflets, something like those of sumac. The flowers are monoecious appearing rather late in spring, just after the leaves unfold, the staminate borne in long pendent simple catkins, the pistillate solitary or



FIG. 38. — Black walnut (*Juglans nigra*), flowering twig.

several together. In North America are found six native species and one, the English or Persian walnut (*J. regia* L.) introduced, probably originally from China, in the middle Atlantic and southern states and, in California.

The pollen grains (fig. 40B) of the different species are all much alike. They are oblatelly flattened, 34 to 42 μ in diameter, provided with 6 to 15 pores (generally about 12) with a decidedly one-sided arrangement, occupying all of the dorsal half of the surface and the adjoining part of the ventral, but leaving a large part of the latter blank. Each pore is surrounded by a thickened rim, those of the neighboring pores almost or quite touching each other so that the whole dorsal surface possesses considerable rigidity while the central part of the ventral surface, which has no pores, is non-rigid and becomes freely invaginated forming a large ventral concavity as the grain dries. The pores are small and elliptical, about 2.5 to 3.5 μ long and so arranged that their long axes converge in groups of threes, or in twos at angles of 20 degrees. The surface of the grain is otherwise smooth except for its fine and faintly granular texture.

The pollen is shed in enormous quantities and in the northeastern states forms a conspicuous element of the atmospheric pollen collected during the last of May and the beginning of June. In the eastern United States are two species, the black walnut (*Juglans nigra* L., fig. 38) and the butternut (*J. cinerea* L., fig. 39). But neither of these, nor the English walnut which is cultivated in part of this area, appears to cause hayfever, though they have occasionally been suspected of doing so.

In California are two native species, the southern California black walnut



FIG. 39. — Butternut (*Juglans cinerea*), flowering twig.

(*J. californica* Wats.) and the California black walnut (*J. Hindsii* Jeps.). Both species are much alike. Indeed, the latter is regarded by many as merely a variety of the former (*J. californica* *Hindsii* Jeps.). They are frequently found around old Indian camp sites. In speaking of the California black walnut, the late Professor H. M. HALL (1918) says: "Much grown as a shade and ornamental tree in Sacramento, Napa, and Russian River valleys; here the most frequent cause of spring hayfever; less common in the San Joaquin valley and the south coast ranges; occurs native especially at Walnut Creek and in the coastal ranges of southern California from Santa Ana mountains north; common in the hills back of Los Angeles and Santa Monica, often near suburban homes. The southern form is var. *Hindsii*,

but the pollen probably reacts interchangeably with the northern form. Pollen produced in great abundance but not carried far from the trees. Positive and virulent. April, May and perhaps early June". These two species, or, as Professor HALL chose to regard them, species and variety, are the only native walnuts of California. The English walnut, however, is extensively cultivated but seems to be here, as in the East, quite harmless to hayfever patients.

Another species similar to and often confused with the California black walnuts is the Arizona walnut or nogal (*J. major* Hell.). It is found on the banks of streams and in the Canyons of central and southern New Mexico and Arizona. Whether or not this is important in hayfever appears to be still unknown. It is generally listed, however, in hayfever studies from Arizona as a possible cause.

Carya (The Hickories)

The hickories are first cousins to the walnuts. Like them, they are tall spreading trees with smooth gray bark, on old trees becoming rough or scaly, with large deciduous pinnate leaves but with generally fewer leaflets than in the walnuts. The flowers are monoecious, appearing after the unfolding of the leaves. The staminate flowers are borne in long pendent catkins which, unlike those of the walnuts, are branched. The genus comprises 17 species of which 15 are found in the United States, one in Mexico and one in southern China. In the United States they are principally eastern and do not occur in the Pacific Coast states.

The pollen grains (fig. 40C) of the different species of hickory are all much alike, spheroidal or somewhat oblately flattened, about 40 to 52 μ in diameter. Their germ pores are generally three, occasionally four or six. Their apertures are short elliptical or nearly circular, with their long axes meridionally oriented, or if more than three, converging in pairs. The pores are always placed slightly dorsad of the equator. Their subexineous thickenings are generally very extensive, being completely fused in the grains of all species examined except those of pecan, but leaving a large part of the surface of the ventral hemisphere free of subexineous thickening, covered only by thin and flexible exine which may be invaginated as the grain dries and shrinks.

The pollen is shed in enormous quantities and is caught on pollen slides in quantities equal to that of the walnuts in the late spring.

Pecan: — By far the most important hickory in hayfever is the pecan (*C. Pecan* Asch. & Graeb.). This is a good example of a tree causing hayfever through cultivation. It grows naturally in the south-central part of the United States, from Iowa to Kentucky to Mississippi to central Texas. It is cultivated in a larger and only partly overlapping area, covering practically the whole of the southern Coastal Plain, from North Carolina to Florida and westward to Texas and Oklahoma. It flowers from mid April to May. Throughout the area of its cultivation where it is used as an orchard and street tree, it causes a great deal of hayfever, often ranking next in importance to ragweed.

The pollen of the other hickories is also known to cause hayfever where the trees are abundant. It is stated by BROWN (1932) to be responsible for quite a few cases in the Middle Atlantic States. The principal species in-

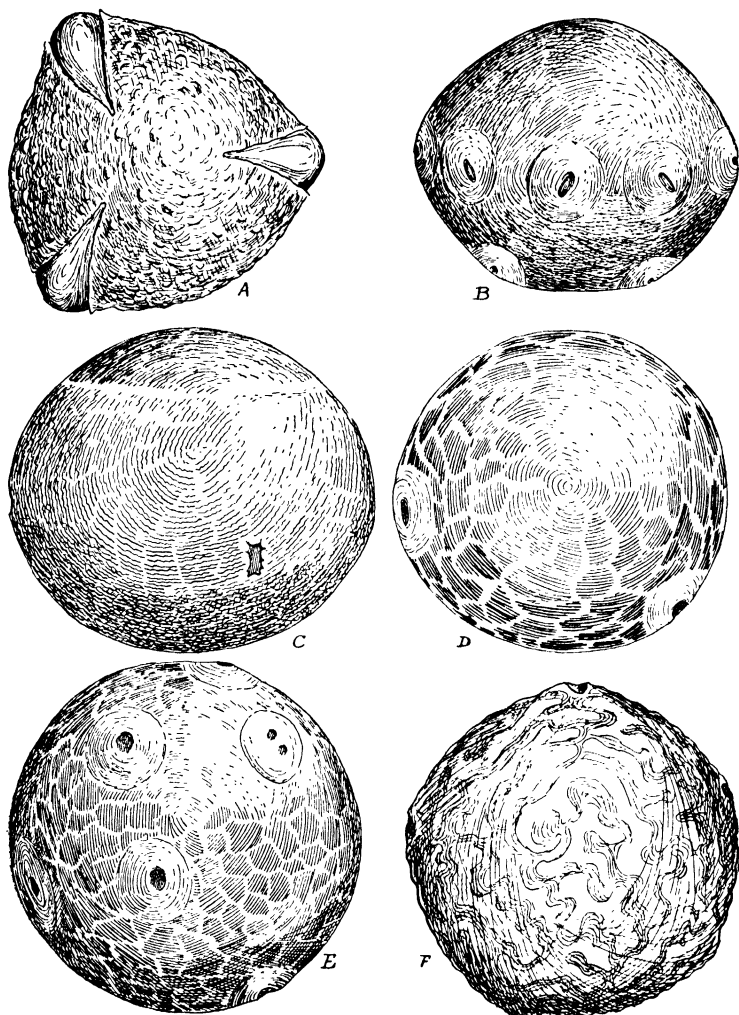


FIG. 40. — SOME TREE POLLEN GRAINS: A, Oak (*Quercus*); B, Black walnut (*Juglans nigra*); C, Hickory (*Carya*); D, Southern hackberry (*Celtis laevigata*); E, Common hackberry (*C. occidentalis*); F, Elm (*Ulmus*). All magnified 1300 times.

volved are the shag- or shell-bark hickory (*C. ovata* K. Koch), the mocker nut or white heart hickory (*C. glabra* Sweet), and the nutmeg hickory (*C. myristicaeformis* Nutt.). In hayfever studies the various species are not

generally distinguished from each other because their pollens are believed to interact more or less perfectly.

Myricaceae (The Bayberry Family)

The bayberry family comprises a small group of aromatic resinous trees and shrubs. The flowers are dioecious or monoecious in unisexual or androgynous catkins with the pistillate near the base and the staminate toward the tip, opening before or with the leaves. All are wind pollinated and shed fairly large amounts of pollen. The pollen grains (fig. 45A) are almost indistinguishable from those of the *Betulaceae*. But this does not mean that the two families are necessarily related. The similarity is more likely due to the extreme adaptation of the members of both families to wind pollination. The family consists of a single genus.

Myrica (The Wax Myrtles)

The wax myrtles comprise about 40 species widely distributed in temperate and warm climates of both hemispheres. Seven are native to North America and the Asiatic *M. rubra* S. & Z. is occasionally cultivated.

The species fall naturally into three groups which could quite properly be regarded as separate genera: (1) The sweet gale or bog myrtle (*Myrica Gale* L.); (2) The bayberries, wax myrtles, candleberries or tallow shrubs (*Certhamnus*), a group of about nine shrubs or small trees producing berries from which wax may be tried out by boiling in water. The best known member of this group in America is the wax myrtle or candleberry (*M. cerifera* L.). This is a shrub or small tree common along the Atlantic coast from New Jersey to Florida and the Gulf coast, also in sandy barrens of the interior. It is the common source of bayberry wax. It is said to be the cause of winter hayfever in Bermuda, together with Bermuda cedar (GAY, CURTIS and NORRIS 1941), and has been suspected in Florida. The small waxberry or bayberry (*M. carolinensis* Small) is a smaller form occurring along the coast from Nova Scotia to Florida, around the Great Lakes and elsewhere in the interior. It is the common form along the Massachusetts coast where it is still used for making candle wax. On the Pacific coast is still another member of this group, the California wax myrtle (*M. californica* Cham.) extending in distribution from southern California to British Columbia, reaching its best development in the region of San Francisco Bay. (3) The sweet fern (*Comptonia perigrina* Coult.), a small shrub with fragrant aromatic fern-like leaves in dry sandy or rocky soils almost throughout North America.

All of these shed large quantities of pollen which possesses the physical characteristics of hayfever pollen. Their role in hayfever is not fully understood and is further confused by the fact that their pollen grains when caught on pollen slides are scarcely to be distinguished from those of the *Betulaceae*.

Ulmaceae (The Elms and Hackberries)

The elm family comprises about 13 genera and 140 species of trees and shrubs of wide distribution. Five genera are represented in North America.

All are wind pollinated and apparently capable of causing hayfever. Besides the three genera discussed below two species of nettle trees (*Trema* Lour.) are found in Florida, and two chaparral trees (*Momisia* Dietr.) in the South from Florida to Texas.

The affinities of the family are not clear. It was formerly regarded as a subdivision of the nettle family (*Urticaceae*). Now it is regarded as a separate family but treated as a member of the order *Urticales* which includes, besides the elm family, the mulberry, hemp and nettle families. Apparently all members of this order are wind pollinated. Consequently both their floral structures and their pollen grains are so far reduced that their relationships are largely obscured.

Ulmus and Planera (The Elms)

The elms comprise 18 or 20 species, mostly trees with deeply furrowed bark. They are widely distributed throughout boreal and temperate regions of the northern hemisphere, but in America are confined to the region east



FIG. 41. — White elm (*Ulmus americana*), flowering twig.

of the Rocky Mountains. Their flowers are small and inconspicuous but perfect, possessing both stamens and pistils. They open either very early, long before the unfolding of the leaves, as do the northern elms, or in the late summer or even in the fall, as do some of the southern elms. They shed large amounts of pollen of high allergenic toxicity.

Their pollen grains (fig. 40 F) are oblatly flattened, 29 to 43 μ in diameter, somewhat angular in outline, provided with four to six pores (generally five except in *U. fulva* in which there are generally four). The pores are elliptical, about 5 μ long and arranged around the equator with their long axes biconvergent. The exine is rather thick and thrown into conspicuous ripple-like thickenings, and generally thicker around the pores. The grains of the water elm (*Planera*) are the same as those of the elms except that there are two band-like thickenings reaching from pore to pore

n sweeping curves, one on each side of the equator, similar in this respect to the grains of the alders.

The commonest species is the white elm (*U. americana* L., fig. 41), a tall graceful tree reaching a height of more than 100 feet, one of the most beautiful trees of our native flora. It is common almost throughout North America east of the Rocky Mountains. It flowers very early, generally in March or April, or earlier in the South. The flowers are so small and inconspicuous that they can scarcely be seen from the ground, though they shed prodigious quantities of pollen. Somewhat similar, though less graceful and smaller, is the slippery elm (*U. fulva* Michx., fig. 42). Its flowers



FIG. 42. — Slippery elm (*Ulmus fulva*), flowering twig.

are borne on short pedicels in crowded capitate fascicles. In the northeastern states is also found the cork or rock elm (*U. racemosa* Thomas). It may be distinguished from the two preceding species by having corky rings on its twigs and branches.

In the southeastern states are found several species of early flowering elms similar to those of the North. The wahoo or winged elm (*U. alata* Michx.), characterized by corky wings on its branches, is common from Virginia to Florida and westward to Illinois and Texas. It is also called red, cork and water elm in allusion to the characters of its bark and its habit of growing in wet places. It flowers in early spring before the opening of its leaves. The Florida elm (*U. floridana* Chapm.) is a small tree with

smooth twigs lacking corky wings, in swamps and low hammocks of the Coastal Plane region from Florida to North Carolina.

Remarkable among the native southern elms are two late flowering species. The cedar or scrub elm (*U. crassifolia* Nutt.) is a small tree with downy twigs, more or less corky winged, and leaves thick and leathery at maturity. It is common from Mississippi to Texas and Arkansas. Its flowers open generally in August or even as late as October. The September or red elm (*U. serotina* Sarg.) is a small tree with downy twigs and corky-winged branches. It is common in Georgia, Alabama and Tennessee where it is occasionally planted as a street tree in cities. It flowers in September. These two late flowering species are known to cause some hayfever, especially the former, and serve to complicate the problem of late summer hayfever in the South.

Besides the native species, the English elm (*U. campestris* L.) has been introduced and is common in New England, and the Scotch elm (*U. glabra* Huds.) is found in the north Atlantic States. The Chinese dwarf elm (*U. pumila* L.) is planted in dry regions as a wind break and has been proved by recent shelter belt experiments at Mandan, North Dakota (GEORGE 1936), to offer the highest resistance to the rigors of that climate.

Celtis (The Hackberries or Nettle trees)

The hackberries are shrubs or small trees with smooth or warty bark. They are wind pollinated, the flowers perfect or monoecious, appearing in the spring at the time of the unfolding of the leaves. Their fruits which are berry-like ripen toward the end of summer.

The genus comprises about 50 or 60 species widely distributed in both temperate and tropical regions, about 8 in North America. It appears that the two commonest species may cause some hayfever. The one generally mentioned in hayfever literature is the common hackberry or sugarberry (*C. occidentalis* L.) also called false elm, beaver wood, hoop ash. It is a small tree with ovate pointed leaves and dark purple fruits, fairly common generally in dry rocky soil from Quebec to North Carolina and westward to Manitoba and Missouri.

The pollen grains (fig. 40E) of this species are extremely various; they range in size from about 30 to 65 μ in diameter and are provided with roundish germ pores varying in number from 3 to 10 and in size from 3 to 7 μ in diameter, and are scattered over the surface without any system of arrangement. Each is surrounded by a weakly developed shield-like thickening or occasionally, if very close, two or more sharing the same shield-like thickening. The exine is smooth or slightly warty-granular.

A similar species is the southern hackberry (*C. laevigata* K. Koch, *C. mississippiensis* Spach) but which may be distinguished by its narrow pointed leaves and orange-red or yellow fruits ripening in September. It is usually a fair-sized tree, reaching sometimes 60 feet in height, in dry soil from Virginia to Florida and westward to southern Illinois and Texas. It flowers in April just as the leaves unfold.

The importance of the hackberries in hayfever appears to be not well understood. They are generally included in lists of hayfever plants or of those with hayfever possibilities as, for example, DUKE (1926). SCHEPPEGRELL (1922) states that hackberry pollen gives reactions with hayfever patients and THOMMEN (1931) states that the most

important hackberry in hayfever is *C. occidentalis*. Tala (*Celtis Tala*) is reported to be an important cause of hayfever in Argentina (WALKER and CARRÓN 1940, CARRÓN and MALVAREZ 1941). WALKER and CARRÓN say it sheds as much pollen as ragweed does in the United States. It is a tree or shrub widely distributed in the central part of Argentina, flowering from September to December. "This pollen was found to be the chief offender in 44 per cent of patients with hayfever."

Moraceae or Artocarpaceae (The Mulberry Family)

The family comprises about 54 genera and 1000 species of monoecious trees or shrubs widely distributed but principally tropical. Four genera are represented in the United States, *Morus*, *Maclura* and *Ficus* native, and *Broussonetia* by introduction from Asia. It appears that the American species, except *Ficus*, are wind pollinated and capable of causing very severe hayfever though cases are relatively infrequent. The relationships between the three following genera appear to be so close that sensitization to the pollen of one implies sensitization to that of the others (BERNTON 1928).

Morus (The Mulberries)

The mulberries are trees or shrubs, monoecious or dioecious with the staminate and pistillate flowers on different branches of the same tree or on different trees, minute, the staminate in elongate cylindric spikes. Each flower has four stamens bent inward in the bud but straightening elastically and becoming exerted at maturity, shedding large amounts of pollen which is occasionally the cause of hayfever.

The pollen grains (fig. 45B) are ellipsoidal or spheroidal, about 20μ in diameter, with generally two, occasionally three, germ pores which are not placed diametrically opposite. The pores are circular, about 3.5μ in diameter, their membranes bulging when the grains are expanded, and capped with a thickening of exine-like material. The exine is thin and smooth or slightly granular. These grains are similar to those of the nettles and paper mulberries but may be distinguished by their larger size.

The genus comprises about 10 species. Only two are native of North America but several others have been introduced. Of the native species the red mulberry (*M. rubra* L.) is a medium sized tree attaining a maximum height of 65 feet. It flowers in April or May and its dark purple red fruit which has a delicious flavor ripens in June or July. It occurs in rich soil in the eastern United States from Vermont to Florida and westward to South Dakota and Texas. The white mulberry (*M. alba* L.) is native of China where it is grown for feeding silk worms. It is also widely cultivated in the United States and Canada occurring in fruit-bearing and ornamental varieties. In its natural form it is a medium sized tree. It flowers in May and bears pink or whitish fruits in July or August. It is sparingly escaped from cultivation in Maine and Ontario and southward to Florida.

The paper mulberry (*Broussonetia papyrifera* Vent., *Papyrius papyrifera* Ktze.), though not a true mulberry, is closely related to the mulberries and its pollen appears to interreact almost perfectly. It is a small to medium-sized tree, wind pollinated, the pistillate flowers borne in dense globular clusters and the staminate in catkin-like spikes. The flowers have the remarkable habit of forcibly ejecting their pollen. Apparently there is some synchronizing mechanism enabling many flowers on the same branch to release their pollen at the same time so that the branches appear to give off periodically puffs of smoke. Its pollen grains (fig. 45E) are similar to those of mulberry but smaller (13.4μ in diameter). It has been shown by BERNTON (1928) to be a potent cause of hayfever.

The paper mulberry is native of China and Japan but extensively cultivated as an ornamental in warm climates elsewhere. In the United States it is thoroughly naturalized throughout the Southeast and as far north as Pennsylvania and west to Oklahoma and Texas. Of it BALYEAT and RINKEL (1932), who have made an exhaustive study of the American distribution of this plant, and the part it plays in hayfever, state that in the southwestern part of Oklahoma it is cultivated for shade in practically every village and city. These authors also furnish a map showing the relative abundance of the tree in the various states of the Southwest. It flowers during the latter part of April or in May.

Osage Orange (*Maclura pomifera* Schneid., *Toxylon pomiferum* Raf.) also called mock orange or bow-wood, is a tree 50 to 60 feet high, bearing pistillate flowers in dense globular clusters and staminate in short loose racemes in June. The fruit which is a large greenish-yellow syncarp about the size of an orange ripens in the autumn. It is most abundant in southern Arkansas to southern Oklahoma and southward in Texas but it is also planted as a hedge plant in the prairie regions of the Mississippi River basin, and in the eastern states.

Its pollen grains (fig. 45C) are oblate spheroidal, smooth, about $19.5 \times 22\mu$ provided with 3 or, occasionally, 4 or 2 germ pores which are small and surrounded by a subexineous thickening, and with their membranes provided with a central thickening. These grains are similar to those of Mulberry except that they are prevailingly three-pored. This pollen appears to interreact more or less perfectly with that of the paper mulberry, and is occasionally a serious cause of hayfever.

Cannabinaceae (The Family of Hemp and Hop)

This family comprises only the hemp and hop. They are herbaceous annuals or perennials with dioecious flowers, entirely wind pollinated. The staminate are borne in paniced racemes, the pistillate in bracted spikes. Both species shed large quantities of extremely buoyant pollen.

The hemp (*Cannabis sativa* L.) is an annual coarse herb with palmately divided leaves, and topped by long spikes of staminate flowers opening from July to September. It is native of Asia but introduced into the United States as a source of fibers which are made into cordage, and as a source of the narcotic drugs marijuana and hashish. It is now extensively escaped in waste places throughout the northeastern states as far south as Georgia and westward to Kansas and Minnesota.

The pollen grains of hemp (fig. 45D) are oblate spheroidal, about 25μ in diameter, with generally three germ pores, occasionally two or four, each surrounded by a subexineous thickening and slightly protruding. Their exine is thin and smooth.

Hemp is undoubtedly an important cause of hayfever in regions where it is abundant. DURHAM (1933d) states that at various places along the Mississippi and Missouri rivers there are areas in which hemp is more common than ragweed, but Omaha is the only place investigated where it was found to assume allergenic importance. MALONEY and BROADKEY (1940) confirm this observation and state that since hemp was introduced into Nebraska in 1889 it has grown wild all over the state, its pollen constituting 17 per cent of the pollen in the air over Omaha during late summer and fall, and 22 per cent of their hayfever cases there were found to be sensitive to it.

Government regulations prevent the use of hemp pollen, except with all the inhibitions imposed by the narcotic laws, though it is doubtful if an appreciable quantity of narcotic is contained in it.

The hop (*Humulus Lupulus* L.) is a perennial vine. It flowers in July and August. Its staminate flowers are borne in paniced tassel-like racemes and the pistillate in pendent cones forming at maturity the familiar hops of commerce. It is native of Europe but cultivated in hop yards and for ornament in America, and is extensively escaped throughout much of the United States and Canada east of the Rocky Mountains. Its pollen grains are indistinguishable in appearance from those of hemp. Their rôle in hayfever is not fully understood.

Polygonaceae (The Buckwheat Family)

The buckwheat family is a large and diversified group comprising about 40 genera and 800 species of herbs, vines and trees. They are all characterized by having jointed stems, usually wrapped at the nodes by united and sheathing stipules. Included in this family are such familiar garden plants as prince's feather (*Polygonum orientale* L.), buckwheat (*Fagopyrum esculentum* Moench) and rhubarb (*Rheum Rapaonticum* L.). Most are herbaceous but the sea grape and pigeon plum of Florida and the Bahamas are small trees. By far the majority are entirely insect pollinated and of little interest to the student of hayfever. The docks and rhubarb, however, are exceptional in being entirely wind pollinated. The docks are generally recognized as hayfever plants but, as far as I am aware, rhubarb has never been shown to cause hayfever.

The pollen grains of the *Polygonaceae* are extremely various among the entomophilous species, and some of them, such as those of the knotweeds (*Polygonum*, *Persicaria*, *Tracaulon* and their relatives) are elaborately sculptured and strikingly beautiful, but those of the anemophilous members, the docks, rhubarb and *Muehlenbeckia* are plain, almost entirely lacking in sculpturing.

Rumex (The Docks)

The genus comprises about 140 species of leafy stemmed annual or perennial herbs. About 35 are native or naturalized in the United States. Their pollen grains (fig. 45F) are spheroidal when moist and expanded, provided with three to six (generally three or four) linear furrows arranged rather strictly according to the trischistoclastic system, each provided with a small elliptical germ pore, and with an exine thin and finely pitted.

Though some docks shed rather large quantities of pollen which is light and easily dispersed by wind, they are relatively unimportant in hayfever. The one generally mentioned in hayfever literature is the sorrel dock (*R. Acetosella* L., fig. 43) also called field, red, wood and sheep sorrel. It is a low perennial herb with fleshy hastate or halberd-shaped leaves with an acrid taste, and dioecious reddish or yellowish flowers which shed large quantities of pollen throughout most of the summer but mostly in May or early June. It is a common weed in dry fields and waste places, particularly

where the soil is impoverished and acid. It occurs practically throughout North America though it is not native, having been introduced from Europe.

Two other species which are fully as common and widely distributed as the sorrel dock are the curly dock (*R. crispus* L., fig. 44) and the broad-leaved or bitter dock (*R. obtusifolius* L.). Both are tall leafy-stemmed perennials, quite different in appearance from the low fleshy sorrel dock, but so similar to each other that it is not always easy to tell them apart, and



FIG. 43. — Sorrel dock (*Rumex Acetosella*).

this difficulty is further increased by the occurrence of natural hybrids between them. Generally, however, curly dock may be recognized by its narrower leaves with curled margins, and the broad-leaved dock by its broader leaves and the lacinate margins of its calyx wings. Both are adventive from Europe and are now spread almost throughout North America. They flower from June to August, but shed much less pollen than the sorrel dock.

In the western part of the United States occurs another species, the canaigre (*R. hymenosepalus* Torr.) which is believed to occasionally cause hayfever. It is a coarse perennial herb growing naturally in dry sandy washes from California eastward to New Mexico. It is also cultivated for



FIG. 44. — Curly dock (*Rumex crispus*).

its large fleshy dahlia-like roots which are used for tanning leather, and its juicy stem which is used as a substitute for rhubarb. As a consequence of these uses it is sometimes known in these regions as pie or sour dock, and wild rhubarb.

Amaranthaceae (The Family of the Pigweeds and Waterhemp)

The amaranth family comprises about 40 genera and 475 species, for the most part weedy herbs, though some exotic genera are low or climbing

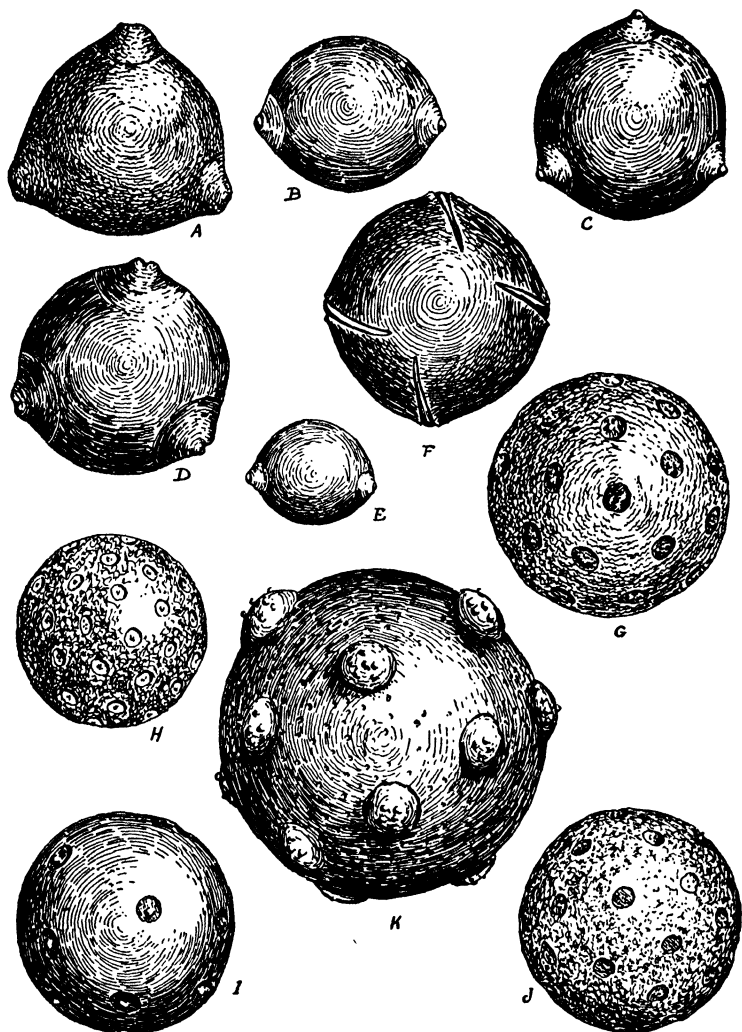


FIG. 45.— POLLEN GRAINS: A, Sweet gale (*Myrica Gale*); B, Mulberry (*Morus*); C, Osage orange (*Maclura pomifera*); D, Hemp (*Cannabis sativa*); E, Paper mulberry (*Broussonetia papyrifera*); F, Dock (*Rumex*); G, Russian thistle (*Salsola Pestifer*); H, Wingscale (*Atriplex canescens*); I, Greasewood (*Sarcobatus vermiculatus*); J, Pigweed (*Amaranthus retroflexus*); K, Sweet gum (*Liquidambar styraciflua*). All magnified 1300 times.

herbs. Some species are wind pollinated, others insect pollinated, but the flowers of all are characterized by extreme simplicity, exhibiting the kind of reduction which comes about through adaptation to wind pollination. The flowers may be perfect or, less frequently, monoecious or dioecious, but they are always small, often greenish or yellowish, and the corolla always entirely lacking. They may have a calyx of two to five sepals but this is nearly always greenish and inconspicuous. Each flower is accompanied by generally three scarious bracts. They are variously clustered, occasionally in long slender open spikes, but more generally in dense terminal spikes or compact axillary heads. In most species the inflorescences are green or straw colored, as among the amaranths and waterhemp, but in some they are white or highly colored and showy, as in the cultivated cockscomb (*Celosia*) and the globe amaranth (*Gomphrena*). The stamens vary in number from three to five. In the amaranths and waterhemp they are entirely separate, but in others their filaments are more or less united, and in some, as for example the globe amaranth, they are united into a long terminal tube forming a sort of substitute corolla.

Apparently anemophily is the primitive condition in this family and entomophily, occurring in the cockscomb and globe amaranth, secondarily acquired. Though nine or ten genera are represented by native species in America only the amaranths and waterhemp are important in hayfever; the others are either too scarce or shed too little pollen. The amaranths and waterhemp are entirely wind pollinated and some of their species shed huge quantities of pollen which causes much hayfever. The globe amaranth, cockscomb and probably most of the cultivated forms appear to be entirely insect pollinated, as suggested by their brilliantly colored flower heads, which are observed to be freely visited by bees.

The pollen grains of most anemophilous species are spheroidal, 25 to 50 μ in diameter, provided with rather numerous germ pores, ranging in size from 2 to 4.5 μ in diameter and arranged at least partly according to the trischistoclastic system. The pore membranes are flecked with granules which are variously distributed but do not tend to aggregate at the center. The exine is thin and more or less granular (fig. 45J). These grains can scarcely be distinguished from those of the Chenopod family, but those of the different species differ from each other in their size and in the size and distance apart of the germ pores.

It has been shown by LAMSON (1931) and by SELLERS and ADAMSON (1932) that the pollens of various species of this family interact almost perfectly with each other and with those of the related *Chenopodiaceae*, showing only slight allergenic differences in some cases.

Amaranthus (The Amaranths or Pigweeds)

The amaranths are annual herbs, usually coarse and weedy though some, such as the prince's-feather, which is a variety of the spleen amaranth (*A. hybridus* L.), and the tassel amaranth (*A. paniculatus* L.), are cultivated for their red or otherwise highly colored panicles and foliage. The flowers are generally monoecious or dioecious but may be bisexual. The stamens are commonly five, occasionally two or three, with their filaments entirely separate. In this latter character they are like the waterhemp

but unlike most other members of the family. Their flowers are always small and inconspicuous, closely aggregated into dense chaffy spikes or panicles, and virtually hidden from view by their subtending bracts.

The genus comprises about 50 species of which about 35 are native of North America and include some of our most important weeds. The weed species appear to be all immigrants to the United States from tropical America. The best known and most ubiquitous of the group is the common



FIG. 46. — Carelessweed (*Amaranthus Palmeri*).

or red-root pigweed (*A. retroflexus* L., fig. 47), also called green amaranth. It is a rough coarse weed from one to ten feet high, with its flowers densely aggregated into thick terminal or axillary spikes. It is common in cultivated or waste soil throughout North America, also in Europe. The flowers shed surprisingly little pollen but in regions where the plants are most abundant it probably causes some hayfever during the latter part of summer.

Often associated with the red-root pigweed but less common, is the

pleen amaranth (*A. hybridus* L.). It may be distinguished by its darker color, reddish stem and often deep red panicles which are long, slender and frequently drooping. Also similar is the carelessweed (*A. Palmeri* Wats.,



FIG. 47. — Pigweed (*Amaranthus retroflexus*).

fig. 46). It may be distinguished by its long slender terminal flowering spikes and the longer petioles of its leaves. It flowers from June to September, shedding much more pollen than the red-root pigweed, and in the region of Missouri, Kansas, Oklahoma and eastern Texas where it is most

abundant, is believed to be important in hayfever. The spiny amaranth (*A. spinosus* L.) is somewhat similar but monoecious with the staminate flowers in long slender spikes and the pistillate in globular clusters in the axils of the leaves. The leaves are rhombic-ovate or ovate-lanceolate with a pair of spines in their axils. The spiny amaranth occurs in waste ground from Maine to Minnesota and southward. In the western and southern parts of its range, where it is most abundant, it occasionally appears to be an important factor in hayfever.



FIG. 48. — Western waterhemp (*Acnida tamariscina*).

Acnida (The Waterhemp)

The waterhempes are similar in appearance and habit to the amaranths but are always dioecious. The calyx of the staminate flowers consist of five thin mucronate sepals longer than the bracts, the pistillate flowers are without calyx. The genus comprises six species native of North America and the West Indies.

The western waterhemp (*A. tamariscina* Wood, fig. 48) is abundant in the prairie region from South Dakota through eastern Nebraska and Kansas to the northeastern corner of New Mexico and south through the eastern half of Texas, and eastward to Indiana. It reaches its maximum abundance in Oklahoma where BALYEAT and STEMEN (1927) find that it is one of the most important causes of late-summer hayfever, the sole cause of 3.6 per cent, and a definite contributing factor in 35 per cent of such cases. They also regard it as "a very important factor in hayfever in the eastern half of Nebraska, the eastern third of South Dakota, many sections of Iowa, some in Illinois, and part of southern Indiana".

A. tuberculata Moq. (*A. altissima* Ridd.) is of similar appearance and habit but the two species may be distinguished by the way in which the fruit, which is a small bladderly utricle, opens; in *A. tamariscina* it dehisces by a regular transverse circular line of division but in *A. tuberculata* it dehisces irregularly. The latter species is less widely distributed, but is abundant in the eastern part of the Dakotas, in Minnesota and Iowa, also in Vermont. Its rôle in hayfever appears to be not fully understood. Of it BALYEAT and STEMEN say, "Since *A. tuberculata* is so closely related to *A. tamariscina*, botanically, it surely must be a factor in the cause of hayfever in districts where it is prevalent. Therefore it is quite probably a factor in many sections of Iowa, southern Wisconsin and eastern North Dakota".

The pollen grains of western waterhemp are somewhat various in size, normally 21 to 28.5 μ in diameter, their pores 2 to 2.8 μ in diameter and 3 to 4.6 μ apart, their membranes flecked with granules which tend to aggregate toward the center and fuse together.

Cladotrix (*Tidestromia lanuginosa* Standl., *Cladotrix lanuginosa* Nutt.) is an annual with clusters of white fuzzy stems, seldom over 16 inches high, and small roundish leaves. It forms conspicuous whitish mats and is a common weed in the high plains, waste places and disturbed areas, western Kansas to Utah, south to northern Mexico.

It has not been shown to cause hayfever, but is wind pollinated and appears to have all the characteristics of a hayfever plant. Its pollen grains are somewhat aberrant for the family, 17.1 μ in diameter, the surface marked off by ridges dividing it into 12 equal pentagonal faces, corresponding to those of a pentagonal dodecahedron, with a pore on each face, their membranes flecked and their margins jagged (illustration WODEHOUSE 1942b).

Chenopodiaceae (The Chenopods or Goosefoots and Saltbushes)

The goosefoot family is closely related to the amaranth family, though not generally similar in appearance. They are mostly fleshy annual or perennial herbs, occasionally shrubs, often succulent and glaucous. Their leaves are alternate, simple, and without stipules. Their flowers are small, inconspicuous and generally greenish; they may be perfect, monoecious or dioecious, but they appear to be always wind pollinated; they are entirely without a corolla but generally have a calyx of three to five herbaceous sepals though even this may be absent in the pistillate flowers of some genera; they are variously clustered, commonly in paniced spikes, with or without bracts which, when present, are never scarious as in the amaranth family.

The pollen grains of all species are much alike and essentially the same as those of the anemophilous *Amaranthaceae*. They are spheroidal, 19 to

33 μ in diameter. The exine is thin and conspicuously granular, provided with round germ pores. These are various in size and number in the different species, and in this are occasionally of diagnostic value. Each is covered by a delicate membrane which is always more or less flecked with granules which tend to be aggregated toward their centers, a circumstance which occasionally serves to distinguish these grains from those of the *Amaranthaceae*.

The family comprises about 75 genera and 550 species of world-wide distribution. Some species shed large quantities of pollen which is undoubtedly a serious cause of hayfever, but most appear to be quite harmless, either because they are not abundant enough or because they shed too little pollen. Most of the troublesome species are introduced weeds of waste places, and of no economic value for they are generally not eaten by stock. As other vegetation is destroyed by over grazing and faulty agriculture many of the *Chenopodiaceae* take over the territory and so are gaining in abundance. On the other hand, two species of the family are of great economic importance. The beet (*Beta vulgaris* L.), a native European species which includes such valuable crop varieties as the sugar beets, mangels and Swiss chard, is widely cultivated in America. It produces greenish or reddish flowers in late summer or fall. The sugar beet appears likely to become an important cause of hayfever in America. DUTTON (1938) reports that beet hayfever is rapidly becoming a major problem in the Mesilla valley of southern New Mexico and western Texas. Severe attacks are suffered by patients from beet pollen encountered by merely driving through the irrigated sections of the valley where the beets are grown, and from the dust that is scattered from threshing the seed. According to PHILLIPS (1939) it already is important in Arizona. Beet-sugar industry has recently been introduced into this state, stimulated by a protective tariff. Since 1936 the acreage devoted to it has increased from 1800 to 5500 acres in 1939. PHILLIPS states that in April and May when the plants bloom they are three to six feet high and look like hedges, and have a sickening sweetish perfume. Pollen production is enormous. "Individuals clinically sensitive to the pollens of other chenopods were found especially liable to acquire sensitivity to beet pollen, but the treatment that protected them against the pollens of amaranth and Russian thistle did not prove a defense against sugar beet pollen. The sugar beet has, in addition to the group atopen common to the Chenopodiales, a potent atopen of its own". Beet pollen grains are about 19.4 μ in diameter with pores 2.75 μ in diameter and 5.6 μ apart.

Similar and closely related to beet is spinach (*Spinacea oleracea* L.). It is domesticated in America from the Old World where it has been cultivated as a pot herb from prehistoric times. It flowers throughout most of the summer, producing a fair amount of pollen which has hayfever possibilities but is not considered important. Its pollen grains are about 30 μ in diameter with pores about 6.5 μ in diameter and 2.3 μ apart.

Among our native species several common weeds of the western prairies and deserts have the appearance of being hayfever plants. The winged pigweed or tumbleweed (*Cycloloma atriplicifolium* Coult.) is common along streams and river banks throughout the central part of the United States from the Mississippi River to the Rocky Mountains. It flowers during most of the summer. The monolepis or poverty weed (*Monolepis Nuttalliana* Engelm.) is a low branching annual weed common in alkaline and dry soil throughout the prairie region of the central part of the United States, flowering from June to September. Winter fat (*Eurotia lanata* Moq.) also called white or sweet sage is found in dry soil, often in desert valleys, throughout the Rocky Mountain region and adjoining plains. The plant is densely silky throughout and forms dense silvery clusters which are conspicuous objects in the plains and table lands of the Rocky Mountains. It flowers from June to September but, though wind pollinated, produces so little pollen that it is probably not important in hayfever. The burroweed (*Allenrolfia occidentalis* Ktze., *Spirostachys occidentalis* Wats.), also called iodine bush or pickleweed, is entirely different; its stems are smooth and succulent, almost glassy in appearance, and its leaves reduced to scales which are tightly appressed against the stems, only gaping apart slightly to allow the anthers of the enclosed flowers to protrude

as they shed their pollen. The pollen grains are about 20.4μ in diameter, with pores about 5.1μ in diameter and 2.8μ apart. The plant is common in salt marshes in Utah, Arizona and southern California, being particularly abundant along irrigation ditches. It flowers from July to September shedding enormous quantities of pollen.

A similar plant, both in its succulent form and in its adaptation to saline situations, is the glasswort or samphire (*Salicornia ambigua* Michx.). It is a low herb with thick jointed leafless stems and opposite branches. The small flowers are sunken in the upper fleshy thickened joints, forming spikes. It is common along both the Pacific and Atlantic coasts. Flowering from May to September, it produces relatively little pollen and is probably of no importance in hayfever. But ROWE and HOWE (1935) in their discussion of the hayfever plants of northwestern California say, "The marshes which bound the inlets and embayments yield large amounts of *Salicornia* pollen". In the West are also several species of *Dondia* or *Sueda*, known as seablites, alkaliblites or seepweed. These are fleshy plants of salt marshes or alkaline plains of California and the Southwest, with something the habit of Russian thistle. *Dondia Moquini* A. Nels. is an especially common weed of the Southwest (PIEMEISEL and LAWSON 1937, SHANTZ and PIEMEISEL 1924). They shed a good deal of pollen in mid and late summer which has hayfever possibilities. HALL (1922) lists *D. fruticosa* Druce among the more important hayfever plants of California, and its pollen was shown by PINES to give reactions with hayfever patients.

The greasewood or chico (*Sarcobatus vermiculatus* Torr.) is an erect shrub one to three feet high with spinescent tangled and matted branches. Its flowers are monoecious or dioecious, the staminate borne in erect catkin-like spikes. It is abundant in dry and saline soils and alkaline flats throughout the Rocky Mountain region south of Montana. It flowers from June to July shedding large amounts of pollen. The grains (fig. 451) are 24 to 30μ in diameter with pores 3μ in diameter and 11μ apart, these grains having the fewest pores of any so far encountered in this family.

Much more important from the hayfever standpoint than any of the above are the two introduced species, Russian thistle and burning bush. Russian thistle (*Salsola Pestifer* A. Nels.), also known as tumbleweed or saltwort, is an annual herb with dryish spine-tipped leaves, divaricately branching, the branches matted together so that the whole plant resembles a gigantic sponge. Toward the end of summer as the plant dries up it breaks off at the root and is rolled about the plains by the wind, scattering its seeds as it goes, until arrested by a fence or some other obstruction in its path. Its flowers are small and inconspicuous, each shedding only a minute amount of pollen, but borne in prodigious numbers. Its pollen grains (fig. 45G) are about 27μ in diameter, with pores about 3.7μ in diameter, which is larger than usual for the family, and 6.6μ apart. Russian thistle has a range extending almost throughout the prairies, much of the Rocky Mountains, and the Great Basin area. It flowers from June to September and is probably the most important cause of hayfever among the *Chenopodiaceae*. It was introduced into this country from Europe or Asia at a comparatively recent date, probably less than a hundred years ago, and is still invading new territory. PIEMEISEL (1932) points out that "Russian thistle is the pioneer on bare lands". That is to say, when the land is broken and its native vegetation destroyed, Russian thistle is the first plant to repossess the area, which accounts for its enormous and rapid spread in recent years.

Burning bush (*Kochia scoparia* Roth), also called fire bush, summer cypress, belvedere and kochia, is somewhat similar to Russian thistle but has longer leaves which are herbaceous and not spine tipped. It is a small and profusely branching annual forming a compact pyramidal bush. Its

symmetrical form and the brilliant red color which its leaves assume toward the end of summer make it a popular plant in formal gardens. It is native of Europe and Asia, but in America has escaped from cultivation and become naturalized locally in fields and waste places in the northern United States. It sheds large quantities of pollen from July to September, and in Colorado where it is thoroughly naturalized and particularly abundant, it is counted among the worst hayfever weeds. Originally escaped from cultivation and a common cause of hayfever only in Colorado, this plant is rapidly spreading eastward. It is now reported by DURHAM (1943) to be a factor of importance in the following states, named in the order of its abundance: Iowa, South Dakota, Wyoming, Colorado, Wisconsin, Minnesota. Its pollen grains are 29 to 30 μ in diameter, with pores about 3 μ in diameter and 6 μ apart. Red sage (*Kochia americana* Wats.) is a native species somewhat similar but only 5 to 11 inches high, with whitish stems and silky leaves becoming smooth at maturity. It occurs in desert valleys from California to Colorado, and is occasionally mentioned as a possible cause of hayfever but its importance has not been established.

Chenopodium (The Chenopods or Goosefoots)

The chenopods are leafy annual or perennial herbs, often white-mealy. The flowers are small but perfect, sessile and bractless, generally tightly clustered into axillary or terminal paniced or compound spikes. Though entirely wind pollinated, they do not shed excessive amounts of pollen, but they sometimes make up for this by their abundance so that the pollen may occasionally be a real factor in hayfever. The grains are 25 to 30 μ in diameter, provided with small pores, 1 to 2.5 μ in diameter and 4 to 5.5 μ apart.

The genus comprises about 60 species, about 20 in America, mostly weeds of world wide distribution. The best known and most frequently mentioned in hayfever literature is lambsquarters (*C. album* L.). It is a tall succulent herb more or less mealy throughout. It is native of Europe but now naturalized throughout North America. In regions where exceptionally abundant it should probably be considered a contributory factor in hayfever. The nettle-leaved goosefoot (*C. murale* L.) is similar in appearance to lambsquarters but may be distinguished by its broader leaf with more sharply toothed margin. It also is widely distributed but generally much less abundant than lambsquarters.

Jerusalem oak (*C. Botrys* L.) is strikingly different in appearance from the two preceding species. It is an erect annual herb, glandular pubescent and with strong disagreeable aromatic odor. The flowers are borne in numerous axillary panicles and the leaves are irregularly pinnately lobed giving them some resemblance in shape to those of some oaks. It is native of Europe and Asia, occasionally cultivated in America and locally established in the northern United States and Canada. It flowers from July to September and may be a factor in hayfever where abundant, particularly westward. Mexican tea (*C. ambrosioides* L., fig. 49) is similar to Jerusalem oak in its glandular leaves and disagreeable odor but differs in appearance; its leaves are generally ovate-oblong with their margins only undulate. It is introduced from tropical America, and abundantly naturalized throughout North America. It flowers from August to October shedding a rather large amount of pollen. The grains are 22.8 μ in diameter,

their pores 1.2μ in diameter and 3.8μ apart, their membranes marked by a single central fleck.

The oak-leaf goosefoot (*C. glaucum* L.) is a low spreading glaucous mealy annual herb with leaves sinuately pinnatifid-toothed, somewhat resembling Russian thistle. It is a European weed, here naturalized in sandy soil and waste places. It flowers in July and August shedding rather large amounts of pollen. It is regarded as an important cause of hayfever in Salt Lake City (BARRETT 1934) and is abundant in the vicinity of Chicago.



FIG. 49. — Mexican tea (*Chenopodium ambrosioides*).

Atriplex (The Saltbushes and Orachs)

The saltbushes are annual or perennial herbs and shrubs with alternate leaves, or the lower opposite, more or less scurfy pubescent. The flowers are monoecious or dioecious, entirely wind pollinated, and inconspicuous, generally aggregated into small compact glomerules which may be axillary or, more often, in terminal spikes or panicles. The flowers of both sexes may

be mixed in the same cluster but more often the staminate are confined to the upper axils or terminal inflorescences.

The pollen grains (fig. 45H) are various in size, 20 to 27μ in diameter with many pores, 2 to 3μ in diameter and 4 to 5.7μ apart, their membranes flecked with several small granules which tend to be aggregated toward their centers, and sometimes completely fused.

The genus comprises about 130 species of wide distribution. About 60 are native or naturalized in America, occupying saline, arid and semiarid soils throughout the continent. According to the classification of HALL and CLEMENTS (1923) which is followed here, the species fall roughly into two groups, monoecious herbs and dioecious shrubs, which are treated as subgenera. The herbaceous group is fairly represented by the gardenscale or garden orach (*A. hortensis* L.) also known as French spinach and cultivated as a potherb (BABB 1939). It is a low herbaceous plant with chenopodium-like leaves, of Old World origin but sporadically escaped from cultivation in America. The shrubby group is fairly represented by the desert holly or hollyscale (*A. hymenelytra* Wats.). It is a compactly branching shrub of alkaline deserts of the Southwest. Its silvery white leaves and branches make it popular for Christmas decorations and for this purpose the plants are shipped east by car loads. The members of the shrubby group correspond to the old genus *Obione*, under which name some of them still occasionally appear in hayfever literature.

Of the saltbushes HALL and CLEMENTS say, "The pollen has been found to be one of the causes of hayfever of the late summer type in the West. Preliminary studies indicate that all species of the group are potential causes of the malady, their relative importance depending more upon the abundance in which the plants grow than upon the specific properties of the different kinds. It does not follow, however, that an individual sensitive to one species is necessarily sensitive to all, since it is found that patients react differently to the pollen of the various species." Fortunately most of the species either do not produce enough pollen or are not abundant enough to be very important. But some of them are potent causes of hayfever.

In the eastern United States the saltbushes may almost entirely be disregarded as factors in hayfever. It is true that several do occur in the East and are recorded in hayfever surveys. These are all small plants and belong to the herbaceous group. For example the sea-beach atriplex (*A. arenaria* Nutt.), a low herb found on sandy beaches from Maine to Florida, and the spearscale (*A. patula* L.), common everywhere in saline soils, salt marshes and alkali flats almost throughout North America (also in Europe, Asia and North Africa). The latter flowers from August to October but sheds pollen only sparingly. It is claimed by ROWE (1928) to be among the most important hayfever plants in the San Francisco Bay region of California but there is no reason to believe that it is of any importance in the East. Occasionally encountered in the southeastern states is the redscale or red orach (*A. rosca* L.). Though occurring only sporadically in the East, it is extremely abundant throughout most of the western half of the United States, particularly along roadsides and in saline places, and according to HALL and CLEMENTS, it is a serious cause of hayfever in these regions. It is naturalized from the Old World but is now the most widely distributed of all the saltbushes in America. It flowers from July to September but sheds relatively little pollen.

Information on the rôle that the different species of saltbush play in hayfever is probably far from complete. The botany of the genus, however,

has been thoroughly worked over by HALL and CLEMENTS (1923) and is presented by them in a logical and easily comprehended form, with notes on hayfever and profusely illustrated. It is mainly from this great work that the materials for this discussion are drawn.

The Australian saltbush or fleshscale (*A. semibaccata* R. Br.) is a prostrate perennial herb becoming woody at the base, with long trailing stems which form dense mats. Its flowers are monoecious, the staminate in small terminal leafy-bracted glomerules, the pistillate solitary or in few-flowered clusters. It was introduced into the United States by the California Experiment Station in 1888 as a forage and hay plant for alkaline districts. It is now thoroughly established throughout much of the Southwest, particularly in the alkaline soils of the San Joaquin and Imperial Valleys and the coastal strip of southern California. Though essentially a halophyte, it readily finds its way along roadsides and in disturbed places. It flowers from June to September shedding large amounts of pollen which undoubtedly causes some hayfever.

Silvery orach or silverscale (*A. argentea* Nutt.) is an erect annual herb, 6 inches to 2½ feet high with monoecious flowers in axillary glomerules, the staminate and pistillate mixed but the former mostly toward the ends of the branches which often end in long spikes of purely staminate flowers. It is one of the most abundant and widely distributed species of the genus, occurring in alkaline soils of western United States and northern Mexico, including most of the Rocky Mountain and Great Basin areas. Occasionally the plants spread from their customary saline habitats and become weeds in fallow fields and disturbed places. The species is extremely variable occurring in several recognizable forms which are treated by many authors as distinct species, and occasionally may be encountered as such in hayfever literature. The most important are *A. caput-medusae* Eastwood, *A. trinervata* Jep., *A. Hillmani* Standl., *A. mohavensis* Standl., *A. nodosa* Greene, *A. Rydbergii* Standl. and *A. volutans* A. Nels. These, however, are at best only varieties of *A. argentea* and are best treated as synonyms. According to HALL and CLEMENTS, however, two distinct subspecies can be recognized *A. argentea typica* (*A. argentea* Nutt.) and *A. argentea expansa* (*A. expansa* Wats.). In the typical form the leaves are all more or less petioled, while in the *expansa* form they are all closely sessile. The typical form is found principally in the region west of Nevada, while the *expansa* form, which is sometimes known as fogweed, is found from California to Texas. Both flower from May to October, principally June and July, shedding large amounts of pollen which is a frequent cause of hayfever.

The bractscale (*A. bracteosa* Wats.) is an annual herb, erect or more commonly prostrate and spreading to form dense mats from which erect stalks arise bearing monoecious flowers, the staminate arranged in naked panicles or spikes. It is common in alkali valleys of California from Sacramento valley south to Lower California, very abundant in the San Joaquin valley and on the coastal slope of southern California, rare east of the Sierra Nevada. HALL and CLEMENTS say of this, "It was originally a moderate halophyte of the distichlis zone especially, but in recent years it has become

the most characteristic weed of disturbed areas in the San Joaquin valley. It often covers fallow fields, roadsides, fenceways, etc. with a dense pure community. The flowers appear from April to October. . . . It is of no value, as it is not eaten by stock, but it is of some importance as a cause of hayfever”.



FIG. 50. — Annual saltbush (*Atriplex Wrightii*).

A closely related species but differing in its more erect habit is the annual saltbush (*A. Wrightii* Wats., fig. 50). It is an annual herb 3 to 4 feet high with monoecious flowers, the staminate in reddish glomerules arranged in long naked terminal panicles. It grows in dense stands in alkaline soils in river valleys, often associated with carelessweed. It also occurs sparingly

along roadsides and as a weed in cultivated fields in southern New Mexico, Arizona and adjoining Mexico. It flowers from June to November and is regarded by WATSON and KIBLER (1922) as one of the most important hayfever weeds in southern Arizona.

Even more important than the herbaceous saltbushes are some of the shrubby species on account of their larger size and the larger amount of pollen that they generally shed. The shrubby species are mostly dioecious, that is to say each bush produces either only staminate or pistillate flowers, but a few species like *A. lentiformis*, are both monoecious and dioecious. They are more highly advanced than the herbaceous species in their adaptation to anemophily and generally shed much more pollen.

Perhaps the best known and most important of the shrubby saltbushes is the wingscale or four-winged saltbush (*A. canescens* Nutt.). This is the one which is generally spoken of in hayfever literature as "Shadscale". The name is a misnomer since it rightfully belongs to *A. confertifolia* of which it aptly describes the pistillate inflorescence. Wingscale is a densely branched shrub, woody throughout, reaching a height of about eight feet, with gray scurfy leaves and twigs, the larger branches dark gray and exfoliating. The staminate glomerules are in dense spikes or long terminal panicles which are leafy below. The species is extremely various and many varieties have received specific names. It is by far the most widely distributed shrubby species of the genus, occurring from Alberta to Kansas, western Texas, Mexico, Lower California, Washington and Montana. According to HALL and CLEMENTS, "While its original rôle was evidently a consociation of the Basin sagebrush association, it occurs in the mixed prairie of the western Dakotas and Nebraska, the desert plains and desert scrub of the Southwest, and in the coastal sagebrush of California". It flowers from early spring to late summer shedding large amounts of pollen which has been shown to be allergenic.

A similar species is the allscale, desert sage (*A. polycarpa* Wats.). It is an erect shrub, woody throughout, 2½ to 6 feet high. The staminate glomerules are borne in axillary and terminal spikes, the pistillate crowded along the numerous divergent branches. It is characteristic of alkali basins in desert areas from southern Nevada, southern Utah, Arizona, adjoining Mexico and southern California, and is particularly abundant in the Mohave and Colorado deserts of western Arizona and eastern California where it is often associated with *A. canescens* and *A. lentiformis*, being only slightly less tolerant of alkali than the latter. It flowers from June to September. Its pollen has been shown to be allergenic and is believed to be an important cause of hayfever in the arid Southwest.

Lenscale (*A. lentiformis* Wats.), also called quailbrush and silver-and-gold saltbush, is an erect woody shrub, 3 to 9 feet high and nearly twice as broad, with spiny branches. It is typically an intense halophyte. According to HALL and CLEMENTS, "Its tolerance of alkali is greater than that of any other plant investigated, and this is in accordance with its dominance in the most alkaline habitats of the Southwest". It is found from the southern half of California to Nevada, southern Utah, New Mexico, Mexico and

the borders of Lower California, and it is particularly abundant in the Colorado and Mohave deserts. It flowers from June to September and appears to be an important cause of hayfever in southern California and Arizona.

The shadscale or spiny saltbush (*A. confertifolia* Wats.) is an erect shrub, woody throughout, rigidly branched and spiny, about 2½ to 7 feet high. It is characteristic of alkaline plains of the western slope of the Rocky Mountains and the Great Basin area where it is the most abundant species on stony planes and hillsides next to sagebrush, and even more tolerant of alkali. It flowers from May to August and is regarded as important in hayfever in Arizona.

Rosaceae (The Family of the Roses, Cherry, Peach and Apple)

The rose family is one of the largest among the flowering plants, comprising more than 100 genera and 2500 species. They are herbs, shrubs and trees with alternate simple or compound, stipulate leaves, their flowers nearly always perfect and regular with five parted calyx and five petaled corolla, generally numerous stamens and one to many carpels.

This family contains many of our most valuable fruit trees, as apple, pear, plum, cherry and peach, and their humbler relatives the raspberries, blackberries and strawberries, and such ornamental trees as the American and European mountain ashes (*Sorbus*), the many different hawthorns (*Crataegus*), cultivated for their showy flowers and bright red fruits which mature in late autumn, and many garden shrubs, as the bridal wreath, steeple bush and meadow sweet (*Spiraea*). Apparently all are insect pollinated though most are somewhat imperfectly adapted to entomophily, producing more pollen than is actually carried away by insects.

The pollen grains (fig. 51A) when expanded are oblate spheroidal, 25 to 52μ in diameter. Normally the grains are provided with three long tapering furrows which function freely in accommodating changes in volume of the grain. The furrows are crossed by a delicate smooth membrane provided with a central germ pore, but the furrow membrane is easily ruptured and is often destroyed in the preparation of the grain for microscopic examination. The exine is always distinctly granular and frequently the granules are arranged in rows presenting a striate appearance similar to that of the grains of some maples. The grains are only meagrely supplied with surface oil so that they do not clump much at time of shedding.

There is no doubt that the pollen of some species possesses allergenic potentialities but the entomophilous habits of the flowers narrowly limit its effectiveness.

Of the whole family it appears that the roses are the most important in hayfever. Their true importance, however, has been largely obscured by the fact that until quite recently many people jumped to the unwarranted conclusion that all early summer hayfever was due to the pollen of roses. Then discovering that most of this was due to grasses, they jumped to the equally unwarranted conclusion that no hayfever was due to roses. Between these all or nothing viewpoints lies the truth that roses can cause hayfever but seldom do, so seldom in fact, that a case of simple rose hayfever is almost a medical curiosity. The former widespread belief in roses as the chief cause of early summer hayfever appears to have an interesting historical significance, being carried over from a time before the agricultural grasses and weeds were as abundant as they are now, and when what little hayfever there was was more often than not caused by the pollen of roses. With the coming of the agricultural grasses and weeds of cultivation, the

roses still held foremost place in the minds of many who saw only the roses, partly because of the inconspicuousness of the real causes and partly because of the very convincing evidence of a few hayfever sufferers who found that smelling roses would cause them to sneeze. In order to avoid this confusion the name "Rose cold" should be reserved for the relatively few cases of hayfever which are actually due to the pollen of roses.

Most roses of modern cultivation are so completely doubled that they produce only infinitesimal amounts of pollen. The doubling of a rose entails the conversion of the stamens, which normally produce pollen, into petals which produce no pollen but enhance the beauty of the flower. It appears that the small traces of pollen that such roses produce is sufficient to affect hayfever patients who handle them, or even the scent alone, as suggested by BIEDERMAN (1937). However, if one wishes to secure rose pollen in any considerable quantity it is a hopeless task to get it from the high bred roses; one must turn to the wild or single varieties. *Rosa rugosa*, a strong rapidly growing stock species upon which many fine varieties are customarily grafted, and which is frequently used as a hedge plant without grafting, is a prolific pollen shedder. Most single varieties and wild species also produce fairly large amounts of pollen.

Besides the roses several species of *Spiraea* have occasionally been thought to cause hayfever, the common hardhack or steeple bush (*S. tomentosa* L.), for example, and such cultivated forms as the bridal wreath (*S. prunifolia* S. & Z.) and *S. Thunbergii* Sieb. The cultivated fruit trees such as the apple (*Pyrus Malus* L.), pear (*Pyrus communis* L.), cherry (*Prunus Cerasus* L.) and the peach (*Prunus Persica* S. & Z.) have occasionally been thought to cause hayfever. Their pollen appears to have the capacity to induce sensitization but the physical characters of both it and the flowers are such that it could become an important factor in hayfever only under unusually close association with the plants.

Platanaceae (Sycamore or Plane-Tree Family)

The Sycamore family comprises only the genus of the plane-trees (*Platanus*). These are tall handsome trees with smooth exfoliating bark, alternate palmately lobed leaves. The leaf petiole is hollow at its base and completely encloses the leaf bud of the following year. The flowers are entirely wind pollinated. They are inconspicuous and open late in spring with the unfolding of the leaves. They shed large amounts of buoyant pollen which is freely caught on pollen slides. The pollen grains (fig. 51B) when fully expanded are oblatelly flattened, 18 to 21 μ in diameter, provided with three or sometimes, four broad furrows with their membranes copiously flecked with granules and without germ pores. The exine is thin and finely reticulate pitted.

The sycamores comprise about 6 species confined to eastern and western North America, Central America and southwestern Asia. They are all similar and closely related, and some have been shown to be important causes of hayfever. The common native sycamore of the East is *Platanus occidentalis* L., also known as plane-tree, button-wood and button-ball. It is particularly abundant along streams and in wet woods and is frequently cultivated throughout the eastern United States and westward to Minne-

sota and Texas. It is one of the largest deciduous trees in the East, reaching a height of 130 feet with a trunk diameter of 14 feet. Its inconspicuous flowers are borne in round heads. Opening in May they shed large amounts of pollen which is abundantly caught on pollen slides, and appears to cause some hayfever; BROWN (1932) states that it is next in importance to the oaks in the Middle Atlantic States.

In California is found another native species, the western sycamore (*P. racemosa* Nutt.). It is generally a smaller tree than the eastern species, scarcely reaching 90 feet in height, and bears its rounded flower heads, both staminate and pistillate, in pendent racemes of three or more. It sheds an abundance of pollen and appears to cause some hayfever. It is common on the banks of streams in western California.

Besides these two native species, the London plane (*P. acerifolia* Willd.), an exotic species of uncertain origin, is much planted as a street tree in the eastern states and in California. This species appears to be sometimes confused with the western sycamore which it resembles but from which it can be distinguished by having its flower heads in twos instead of in racemes of three or more. It is also sometimes confused with the oriental plane-tree (*P. orientalis* L.), an Asiatic and European species which is only rarely grown in America. The London plane-tree is regarded by HALL (1922) as a cause of hayfever in California.

Mimosaceae (The Mimosas, Acacias and Mesquites)

The mimosa family comprises about 40 genera and more than 1500 species of herbs, shrubs and trees, mostly of tropical distribution. They are considered to be closely related to the *Fabaceae*, and are by many authors joined with them, the *Caesalpiniaceae* and *Krameriaceae*, to form the family *Leguminosae*. The flowers are small with generally a minute calyx and corolla, and are borne in dense heads or spikes. The stamens are numerous, their filaments long, protruding much beyond the corolla and giving the flowers the appearance of being anemophilous. There seems to be no doubt, however, that they are primarily, if not entirely, entomophilous. Those of many species are sweet scented, brilliantly colored and attract insects and, what is even more important, most species produce relatively little pollen in spite of their numerous stamens.

The pollen grains of this family exhibit an enormous diversity of form, those of some of the different genera having no visible resemblances to each other. This seems to be due to the fact that the grains of most species are variously compounded in groups of four or multiples of four, the union exerting so strong an influence on their form that their basic phylogenetic characters are largely suppressed. The grains of the sensitive plant (*Mimosa pudica* L.) are united in compact tetrahedral tetrads. They are extremely small, the whole tetrad measuring only 9 to 9.5 μ in diameter. Their exine is thin and exhibits no trace of pores or furrows. The grains of *Acacia* (fig. 51D) are further compounded, generally occurring in groups of 16, composed of four united tetrads. But the grains of *Acacia* pollen are considerably larger, the individual cells measuring about 17 μ in diameter, and the germinal furrows, though only vestigial and entirely functionless, conform in their arrangement to the trischistoclastic system as far as its expression is possible under the limitations imposed by the union of the grains. The grains of mesquite (fig. 51C) always occur singly, and they

conform in every respect to the basic form of the *Fabaceae* and, in fact, the other *Rosales* with which this family is associated, characterized by three meridionally arranged furrows without pores, and with faintly granular exine. There is no doubt that mesquite is closely related to *Mimosa* and *Acacia*, yet the form of its pollen grains is of the type one would expect to find in association with the *Rosales* instead of being

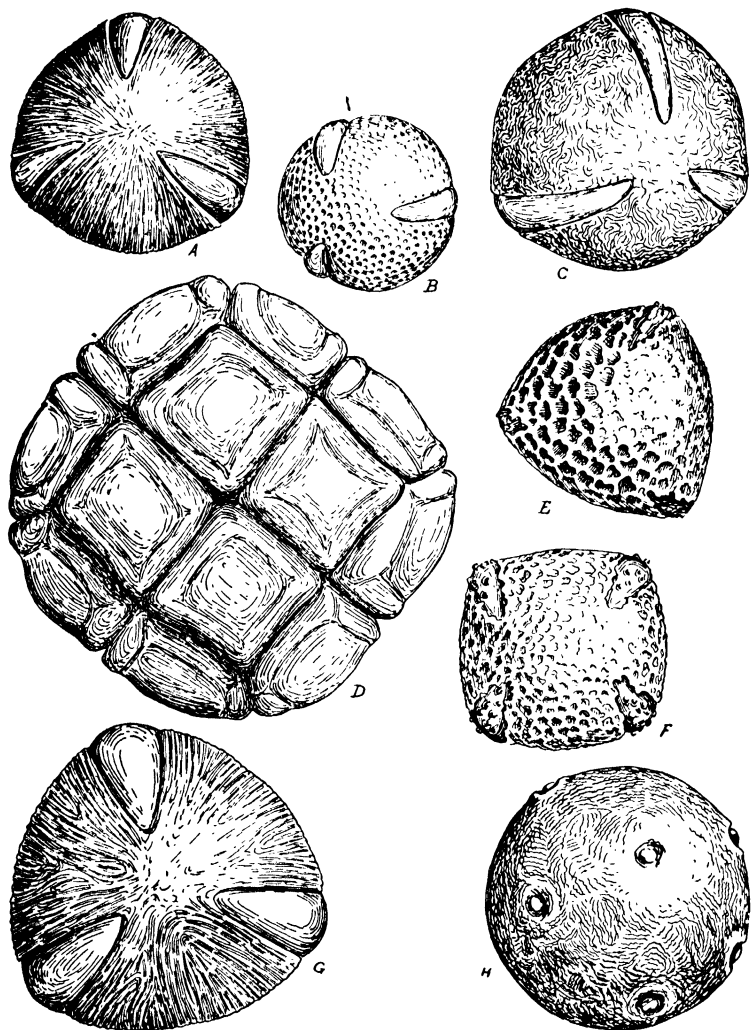


FIG. 51. — POLLEN GRAINS: A, Rose (*Rosa rugosa*); B, Sycamore (*Platanus*); C, Mesquite (*Prosopis glandulosa*); D, Acacia; E, Olive (*Olea europaea*); F, White ash (*Fraxinus americana*); G, Norway maple (*Acer platanoides*); H, English plantain (*Plantago lanceolata*). All magnified 1300 times.

like those of *Mimosa* and *Acacia*. So it seems logical to deduce that the extreme modification of form encountered in the grains of *Mimosa* and *Acacia* is the result of their compounding.

Only the acacias, mimosa tree and mesquite of this family have ever been suspected of causing hayfever and even they can be of only relatively little importance.

Acacia

The acacias comprise about 450 species, not always clearly defined, of small trees or shrubs, widely distributed throughout the tropics, especially in Australia. Several species are native of America, characteristic of the hot and arid regions of the Southwest. One of the best known is the opopanax or huisache (*A. Farnesiana* Willd.), also called popinack and cassie. It is a small tree, 20 to 30 feet high, with spreading spiny branches bearing bright yellow flowers closely compacted in small globular heads, opening in February and March. It occurs naturally from Texas to Chili, but is now distributed through introduction almost throughout tropical and subtropical regions. Though the flowers present the appearance of being wind pollinated they are probably not, for they are so sweetly scented that the plant is cultivated in the Mediterranean region for its perfume.

In the warmer parts of the United States, especially California, several species of *Acacia* are grown for ornament, for example the Sydney golden wattles (*A. longifolia* Willd.) with beautiful yellow flowers in long axillary spikes, as much as $2\frac{1}{4}$ inches long. In hothouses throughout the world many other species are grown.

The status of acacia pollen as a cause of hayfever appears to be not quite clear. Of it HALL (1922) says: "Popularly supposed to be a cause of spring hayfever, but this is almost impossible except by direct inhalation. The pollen is produced very sparingly and is not easily carried by the wind". The popular belief in its hayfever producing proclivities, however, is probably not entirely unfounded, for ROWE (1928) says, "*Acacia* pollen, though usually carried by insects, has been found on our plates, and it causes definite hayfever and asthma in some cases". Later ROWE (1931) finds that the pollen, though occurring only in small quantities is extremely toxic: "It produces not only hayfever and asthma but dermatitis and pollen toxemia". Also DEAMER and MCMINN (1935) report *Acacia* pollen on their pollen plates from various parts of San Francisco. These reports, however, are still open to question.

Prosopis (The Mesquites)

The mesquites are deciduous shrubs or small trees, armed with spines or thorns. They resemble the acacias and appear to be very closely related to them. Their flowers are like those of acacia but with separate petals and only 10 stamens. Two species are common in the arid regions of America.

The honey mesquite (*P. juliflora* DC., *P. glandulosa* Torr.), also called honey locust and algaroba, is a low spreading shrub with a large thick tap-root which is said to descend to a depth of 40 to 50 feet and with rudimentary

horizontal roots spreading in all directions. On account of its extraordinary root system the plant is able to survive and maintain a flourishing green crown in almost the driest deserts, and is perhaps the most characteristic shrub of the arid regions of the Southwest from Louisiana to Arizona and Mexico and northward to Kansas. It flowers from May to July, producing spikes of minute greenish yellow flowers which are sweet scented and undoubtedly primarily insect pollinated but strongly suggest by their appearance and the large amount of pollen that they shed that they may also be partly wind pollinated. There also seems no doubt that this pollen can produce hayfever. Of it SELLERS (1934) says: "In wide areas of west Texas the most important tree causing hayfever in the spring is the mesquite. This tree begins to pollinate in late April and continues to do so intermittently until July. Its pollen is both wind and insect borne". This same author in an earlier article (SELLERS 1929) reports 10 cases in Texas having symptoms of hayfever starting in April or early May and continuing at irregular intervals throughout the summer, which were definitely proved to be due to mesquite and were benefited by treatment with its pollen. In a discussion of this article, Dr. I. S. KAHN reports that in Honolulu mesquite is claimed to cause a good deal of hayfever.

The wood of the mesquite has been demonstrated to cause dermatitis (Fox 1941).

The screw-pod mesquite, Mexican screw bean or tornillo (*P. pubescens* Benth., *Strombocarpus pubescens* Gray) is of similar habit and appearance but may be distinguished by its tightly curled seed pods. It occurs in sandy and gravelly washes from Texas to southern California, north to Colorado and Nevada, and in Mexico. It is common in the Colorado and Mohave deserts and even in parts of Death Valley. It flowers from early spring to midsummer and, like honey mesquite, suggests by the appearance of its flowers that it may be partly wind pollinated, but it is not known to cause hayfever.

The mimosa tree (*Albizia Julibrissin* Durazz.) is a shrub or small tree with scaly bark, and leaves twice pinnately divided giving them a fern-like appearance. It bears large clusters of pink or whitish flowers during spring and most of the summer. It is native of Asia but now widely cultivated and naturalized in the South from Virginia to Florida and Louisiana. It is not known to cause hayfever but has occasionally been suspected of doing so. Its common name of mimosa is a survival from a time when it and the acacias were included in the genus *Mimosa*.

Fabaceae (The Pea Family)

The pea family comprises about 325 genera and more than 5000 species of herbs, shrubs, vines and trees, with compound leaves and irregularly papilionaceous flowers. All are entirely insect pollinated and most of them remarkable for the perfection of their adaptation to entomophily. They shed only minute quantities of pollen and their stamens are generally concealed in the fold of the lower petal in such a way that their anthers can not be exposed except by the action of an appropriate insect releasing the

mechanism. It seems unreasonable to look for causes of hayfever among plants in which the pollen is so efficiently guarded and dispensed, yet several species have been suspected and apparently with some justification.

One of those most frequently blamed for hayfever is alfalfa (*Medicago sativa* L.). It is a much branched spreading herb resembling clover, with deep violet or blue flowers during most of summer. It is native of Europe but much cultivated for fodder and hay almost throughout the United States. The stamens are held at maturity under tension but so arranged that they may be tripped by a visiting insect when the anthers strike him on the thorax (BRINK and COOPER 1936). It would thus appear unlikely that under normal conditions enough pollen could ever become scattered in the air to become atmospheric. Still FOSKETT (1929) reports two hayfever cases found to be sensitive to alfalfa pollen. They lived with alfalfa plants growing right up to their door. Upon being treated with an extract of alfalfa pollen they were relieved of their hayfever. ELLIS and ROSENDAHL (1933) point out that alfalfa and clover are cut and cured at their time of bloom and much shattering of flowers undoubtedly occurs offering the possibility of hayfever from the curing of alfalfa hay.

Several clovers (*Trifolium*) have attracted attention as possible causes of hayfever but probably with still less justification. One of the commonest is the beautiful red or purple clover (*T. pratense* L.), a European species which may be found flowering from early spring to late fall in moist fields and meadows throughout most of the United States. Often associated with it is the pink or alsike clover (*T. hybridum* L.) and the white, Dutch or honeysuckle clover (*T. repens* L.).

White and Yellow sweet clovers (*Melilotus alba* Desv. and *M. officinalis* Lam.) are naturalized and widespread weeds, flowering throughout the summer. It is probably only on account of their abundance and close association with human habitations that they have been accorded a place in hayfever literature.

Among the arborescent forms of the *Fabaceae* the locust (*Robinia pseudoacacia* L.) is sometimes given consideration in hayfever studies but, like the other members of the family, it could only cause hayfever under most unusual circumstances.

The pollen grains of the pea family are somewhat various. They are prevailing three furrowed and their exines are striate or finely reticulate. The grains of alfalfa and sweet clover can easily be distinguished by their size and the markings of their exines (WODEHOUSE 1942b, Pl. VIII, 79, 80). JAMIESON (1939) states that the grains of *Trifolium hybridum* can be distinguished from those of *T. repens* and from those of alfalfa by the degree of coarseness of the reticulum of their exines.

Simarubaceae (Ailanthus or Quassia Family)

The ailanthus family comprises about 150 species in 30 genera of trees and shrubs mostly native of warm or tropical regions. Its only interest from the hayfever standpoint is through the tree-of-heaven (*Ailanthus altissima* Swingle). This is a small to medium-sized tree much planted for its attractive and exotic appearance which it owes partly to its long pinnate leaves, 1 to 3 feet long, with 13 to 41 leaflets, and partly to its large panicles of ill scented greenish-white flowers which are produced in June. They are primarily insect pollinated, but they are obviously only poorly adapted to entomophily, for much pollen is liberated to be blown away by the wind, and is readily caught on atmospheric pollen slides during most of June.

Its pollen grains (fig. 58A) when moist are oblatelly flattened, about 26μ in diameter, provided with three long tapering germinal furrows with smooth membranes and each with a clearly defined germ pore. The exine is rather thick and coarsely reticulate with the reticulations tending to be linearly arranged.

The tree is native of China but escaped from cultivation and thoroughly naturalized practically throughout the United States, and in many places is regarded as a pest. It is said to cause hayfever in China and has recently been reported as doing so in the United States (BLUMSTEIN 1943).

Tiliaceae (Linden Family)

The linden family comprises a large number of trees and shrubs of world-wide distribution. But they are represented in the United States by only three genera, *Corchorus* and *Triumfetta* of extreme southern regions, and *Tilia* of more northern distribution. Only the latter has ever been given serious consideration as a cause of hayfever.

Tilia (Linden, Basswood)

The basswoods are fine trees with soft white wood, broad heart-shaped leaves and showy white or cream-colored flowers borne in clusters subtended by a large leaf-like bract. The flowers are peculiarly fragrant and notable for the large amounts of honey obtainable from them. Though entirely insect pollinated they are copious pollen shedders and their pollen can easily be demonstrated in the air at considerable distances from the flowering trees. That it could occasionally cause hayfever is to be expected. Indeed DERBES (1941) has reported such cases.

Several species occur naturally in the United States. The most abundant is *T. americana* L., Basswood or Whitewood, widely distributed throughout the eastern half of the United States. The European linden (*T. europaea* L.) is most frequently cultivated in and near cities as a shade tree. It occurs in several varieties which are selected by horticulturists for various purposes.

The different species and varieties of linden may flower at widely different times so that their flowering period extends over several months, from May to July.

Linden pollen grains are uniform in size, lens shaped, about 36.5μ in diameter and 28μ thick. They are provided with three, or occasionally four, germ pores deeply sunken in their short pit-like furrows. The exine is rather thick and finely reticulate. There is no other atmospheric pollen grain which those of *Tilia* even remotely resemble.

Aceraceae (The Maple Family)

The maple family comprises only the maples and the single Asiatic species, *Dipteronia sinensis* Oliv., which is native of central China but occasionally cultivated as an ornamental in the warmer parts of the United States.

Acer (The Maples)

The maples are trees or shrubs with watery sap which is often sugary, comprising about 115 species of wide distribution over most of the northern

hemisphere and, in one species, extending south of the equator in the mountains of Java. The leaves and twigs are opposite or occasionally in whorls of three. The leaves are long petioled, simple, palmately 3 to 7 lobed or nerved, or in one species 3 to 7 foliate. Some species are entirely entomophilous and one (*A. Negundo*) entirely anemophilous, but most appear to be amphiphilous, exhibiting various degrees of adaptation to pollination by both insects and wind. The flowers are regular but only occasionally all perfect. There appears to be a rough correlation between the completeness of the separation of the sexes and the degree of adaptation of the flowers to wind pollination.

The pollen grains of the maples (fig. 51G) are rounded triangular or spheroidal and oblatelly flattened when fully expanded. They have usually three furrows which are long and tapering to pointed ends, almost meeting at the poles, their membranes smooth and without germ pores. Usually there are some grains with supernumerary furrows which may or may not conform to the trischistoclastic system. The exine is finely reticulate pitted or granular, the one condition sometimes shading into the other on the same grain. The granules or pits may or may not be linearly arranged in striae which assume the form of thumb-print markings. In the grains of *A. platanoides* the exine is rather thick and definitely and constantly striate. In those of *A. Pseudoplatanus* the exine is thinner but still striate. In those of *A. rubrum* the exine is fully as thick and even more markedly striate than in the grains of *A. platanoides*. But in those of *A. saccharinum* and *A. saccharum* the exine is thinner and not consistently striate, the majority of the grains showing no trace of striae, and in those of *A. Negundo* the exine is very thin and entirely without striae. The grains with the thickest and most definitely striate exines are found among those whose flowers are mostly or entirely insect pollinated and those with the thinnest and least striate exines are found among those whose flowers are nearly or entirely wind pollinated.

Entomophilous Species: — Among those which appear to be entirely entomophilous are the Norway maple (*A. platanoides* L.). It is native of Europe but throughout most of the United States is a favorite tree for street planting and as an ornamental in parks and gardens. It occurs in many forms which are much prized in cultivation for the color of their leaves and the way in which they are cut. The flowers, which open in May at about the same time as the leaves, present the appearance of being completely entomophilous. They are about $\frac{1}{3}$ inch in diameter, provided with calyx and corolla, greenish yellow in erect or nodding many flowered, stalked corymbs. There is only a slight tendency toward the separation of the sexes, both perfect and unisexual flowers occurring on the same or different trees, a condition spoken of as andropolygamous.

Similar in these respects is the sycamore maple (*A. Pseudoplatanus* L.). Its flowers are also andropolygamous, greenish yellow and with both calyx and corolla, but somewhat smaller, and are borne in pendulous racemes, $2\frac{1}{2}$ to 5 inches long, appearing late in May after the leaves have almost

fully developed. It is a medium-sized round-topped tree, native of Europe and Asia where it has been cultivated for centuries. In the United States it is a favorite for street and park planting. While both of these trees are probably entirely insect pollinated, their adaptation to this mode of pollination is obviously imperfect, and some pollen is scattered and may appear in the air in sufficient quantity to become at times a factor in hayfever.

Amphiphilous Maples:— Among those which appear to be partly pollinated by insects and partly by wind are such familiar trees as the red maple, silver maple and sugar maple. These have flowers which are attractive to insects, but their stamens are exserted and shed more pollen than is carried off by insects, and it can easily be detected in the air. Of these the



FIG. 52. — Red maple (*Acer rubrum*), flowering twig and enlarged flower.

red maple (*A. rubrum* L., fig. 52) also called scarlet, white, swamp or soft maple, is a handsome tree from 80 to 120 feet high. It is one of the commonest and most generally distributed in North America. It occurs principally in rich moist soil, taking readily to swamps, throughout the eastern states and westward to Manitoba and Texas. It flowers from March to April, its bright scarlet or yellowish flowers appearing long before the leaves. The flowers are small, the staminate and pistillate aggregated in different fascicles on the same or different trees. Each flower is provided

with a small calyx and corolla beyond which the stamens protrude. They are sweet scented and eagerly sought by bees. Nevertheless the pollen is scattered in the air and may at times become a menace to hayfever sufferers.

The silver maple (*A. saccharinum* L.) also called white, river, soft or swamp maple, is similar in appearance and habit to the red maple, but it flowers earlier, generally in February and March, depending upon the locality and season, and its flowers are yellowish green. They are sessile or short stalked and closely aggregated in fascicles. The calyx is minute and five lobed, as in *A. rubrum*, but the corolla is entirely absent. The stamens are prominently exserted and the staminate and pistillate flowers in different clusters on the same or different trees. The silver maple is a tall handsome tree, 90 to 100 feet high, abundant throughout the eastern states and as far west as the Dakotas and Oklahoma. It occurs in several varieties which are favorites for street planting. It is also sometimes used as a source of



FIG. 53. — Sugar maple (*Acer saccharum*), flowering twig.

sugar but said to be less satisfactory than sugar maple. It appears to be primarily insect pollinated but less so than its close relative the red maple.

The sugar maple (*A. saccharum* Marsh., fig. 53) also called rock, hard, black or sweet maple is both wind and insect pollinated. The flowers open at the same time as the leaves in April or May. They are borne on long drooping pedicels in nearly sessile umbel like corymbs. Each little flower is provided with a five lobed calyx greenish yellow in color, but with no corolla. The staminate and pistillate flowers are in the same or separate clusters on the same or different trees. The stamens have unusually large anthers which protrude from the calyx suggesting a strong tendency toward anemophily. They are, however, freely visited by bees so they are at least partly entomophilous.

The trees are large and stately components of our deciduous forests from Newfoundland to Florida and westward to Texas. There occur

several varieties which are much prized for street and park planting. This species is the source of most of the maple sugar.

Anemophilous Species: — The boxelder (*A. Negundo* L., *Negundo aceroides* Moench, *Rulac Negundo* Hitchc., fig. 54) also known as ash-leaved or cutleaved maple, or water ash, is undoubtedly entirely wind pollinated. Its flowers, which expand just before the leaves, in April, are yellowish green borne on long slender drooping pedicels, the staminate in ascicles, the pistillate in narrow drooping racemes, those of the two sexes on different trees. Each little flower is provided with a minute five-lobed



FIG. 54. — Boxelder (*Acer Negundo*), flowering twig.

calyx and 4 to 6 stamens but no corolla and the stamens with their large anthers hang out beyond the calyx and appear to shed much more pollen than those of any other maple.

Boxelder is a small to medium-sized tree, seldom reaching over 70 feet, generally wide spreading with the trunk dividing near the ground. Its most distinctive character is that of its leaves which are usually divided into three, occasionally five to seven, leaflets. It is found growing naturally along the banks of streams and lakes and the borders of swamps throughout eastern North America as far west as Nebraska and Texas, and is exten-

sively planted as a street tree in the cities of Utah and used as a windbreak in the Missouri valley states. Near the Atlantic coast it is frequently planted along streets and in parks but is otherwise scarce. It also occurs in the Rocky Mountain region from Saskatchewan to Mexico, and in California. The trees of these regions are slightly different and are designated respectively as var. *interior* Sarg. and var. *californica* Sarg.

Oleaceae (Olive Family)

The olive family comprises about 400 species in 20 genera of trees and shrubs. Most are entirely insect pollinated and of little interest in hayfever studies. Some are cultivated for the beauty and fragrance of their flowers. Among such are the lilac (*Syringa*), an Asiatic genus of which some five or six species and many varieties are cultivated in America, and the jasmins (*Jasminum*), a huge genus of tropical climbing or erect shrubs of which about fifteen species are cultivated particularly in the southern states, and goldenbells (*Forsythia*), well known to all as the first flowers of the garden to appear in spring. These are all closely insect pollinated and could hardly be considered as hayfever plants though they have occasionally been suspected. On the other hand the olive and privets, though obviously entomophilous, are only imperfectly adapted to this mode of pollination so that much pollen escapes into the air. The ashes are some insect and some wind pollinated and are of real importance in hayfever.

The pollen grains of the *Oleaceae* considered here are spheroidal or oblatelly flattened and with three meridionally arranged furrows (occasionally four or more) without well defined pores. The exine is variously but always conspicuously reticulate (WODEHOUSE 1935).

Olive (*Olea europaea* L.) is a small spreading tree about 25 feet high with tough evergreen leaves dark above but silvery and scurfy below, arranged oppositely on the branches. The flowers appearing in April and May are small and white, dioecious or polygamous, somewhat resembling those of privet but sweet scented. They are undoubtedly primarily insect pollinated but appear to be also partly wind pollinated for they scatter large amounts of pollen which is known to cause some hayfever in parts of California and Arizona where the trees are extensively grown for their fruit (PHILLIPS 1932).

Their pollen grains (fig. 51E) are about 22μ in diameter, with generally three or occasionally four furrows which have jagged margins and flecked membranes. The mesh of the reticulum is rather coarse, coarser than that of the grains of *Fraxinus* but less so than in those of *Ligustrum*.

Ligustrum (The Privets)

The privets are deciduous or evergreen shrubs with opposite leaves, bearing numerous small white flowers in compact terminal panicles, resembling those of lilac but less showy, and disagreeably scented. Their flowers are undoubtedly primarily insect pollinated but their adaptation to this mode of pollination is so loose that they may even be partly wind pollinated; if a flowering privet bush is shaken on a still day quantities of pollen can be seen to float away in the air. Privet pollen is frequently caught on atmospheric pollen slides and has been shown to be an important cause of

hayfever in regions where the bushes are abundant and allowed to flower. (SCHEPPEGRELL 1925).

The pollen grains are similar to those of olive but with thicker and more closely reticulate exine and with their furrows more sharply defined.

The genus comprises about 50 species, native of Asia, Australia, and one in the Mediterranean region. About a dozen are cultivated in America, planted for their ornamental foliage or their flowers which open mostly in late spring or early summer,



FIG. 55.—Privet (*Ligustrum ovalifolium*), flowering twig and enlarged flower.

or for hedges in which case they are generally prevented from flowering by frequent clipping.

The California privet (*L. ovalifolium* Hassk., fig. 55) is the one most usually cultivated in the North. When used as a flowering shrub it may reach a height of 15 feet or more, bearing numerous panicles of white flowers in June and July. The flowers are tubular like those of lilac, each with two stamens with their anthers projecting beyond the corolla so that if the pollen is not carried away by insects it is easily scat-

tered. The common privet (*L. vulgare* L.) is similar but may be distinguished by its shorter corolla tube with the stamens included; also it is entirely deciduous while the California privet is partly evergreen. Both species occur in several varieties, some with leaves yellow or variegated with white, which are used as ornamentals and for hedges.

The ibota privet (*L. Ibota* Sieb.) is also frequently cultivated. It is a smaller and more graceful shrub with pubescent branches and leaves pubescent on the under side; it is an attractive garden shrub and has an advantage in not shedding nearly so much pollen as common or California privet.

The southern or glossy privet (*L. lucidum* Ait.) is the species most frequently planted in the South. It is a shrub or small tree with thick leathery evergreen leaves and small white flowers opening in spring. It appears to have hayfever possibilities similar to the California privet.

In hayfever studies the species of privet are rarely distinguished from each other so it is not known if there are allergenic distinctions between their pollen.

Fraxinus (Ash)

The ashes comprise about 65 species of deciduous trees mostly of the north temperate zone, with opposite usually pinnate leaves and opposite branches. Their flowers are various, depending upon their mode of pollination. Of those which are insect pollinated the flowers are perfect with corolla, and fragrant, somewhat resembling those of privet and olive, and appearing in spring with or after the new leaves. Such a tree is the flowering ash (*F. Ornus* L.), a handsome tree bearing fragrant white flowers in May and June, native of southern Europe and western Asia, but frequently cultivated in the warmer parts of the United States. A similar species is the native *F. cuspidata* Torr., a shrub or small tree of western Texas and New Mexico, with fragrant white flowers appearing in April. It is regarded as a possible cause of hayfever (WATRY and LAMSON 1934). There are also several Asiatic species occasionally cultivated in America which, like *F. Ornus* and *F. cuspidata*, are insect pollinated. But the majority of ashes in America are entirely wind pollinated and notorious for the large amounts of pollen which they shed. These have unattractive flowers without corollas and even sometimes without calyces. Many of them are handsome trees, frequently used in street and park plantings. And they constitute a real menace to hayfever sufferers, sometimes counted among the most important hayfever trees.

The pollen grains (fig. 51F) of *F. americana* and *F. velutina* are 20 to 25 μ in diameter, flattened and angular in outline with generally four, less often three or five, furrows, one at each angle, their membranes flecked and margins jagged. The exine is thin with its reticulum less strongly developed than in the grains of other members of the family and ending along the furrows with open lacunae.

White ash (*F. americana* L.) is a tall forest tree reaching over a hundred feet in height, with dioecious flowers opening in spring just before the leaves, and shedding huge quantities of buoyant pollen. It occurs in moist rich soil almost throughout the United States east of the Rocky Mountains, reaching its best development in the bottom lands of the basin of the lower

Mississippi River; northward and westward of the Mississippi River it is less common and of smaller size.

Red ash (*F. pennsylvanica* Marsh.) is a similar tree but smaller, 40 to 60 feet high, flowering late in spring just as the leaves begin to unfold, and with similar distribution, reaching from Nova Scotia to Manitoba and southward to southern Georgia, Alabama and Mississippi. The species is very variable and several varieties have been recognized. Perhaps even better known than the species itself is the green ash (*F. pennsylvanica lanceolata* Sarg.). By some this is regarded as a distinct species and known as *F. lanceolata* Borkh. or *F. viridis* Michx. f. It is a small tree seldom more than 60 feet high with ashy gray branchlets marked by pale lenticels. It has a more southerly distribution, from Maine to Florida and westward to Saskatchewan, Montana and Texas, most abundant in the basin of the Mississippi River and eastern Texas, and appears to be the most important ash of the South. It is one of the seven species of trees found capable of surviving the rigorous climate of the shelter belt at Mandan, North Dakota, showing there a resistance second only to that of the Chinese elm (GEORGE 1936).

Mountain ash (*F. texana* Sarg.) is a small tree, rarely reaching 50 feet in height, with stout dark green branches tinged with red, and downy when young, flowering in March as the leaves begin to unfold. It is found on the high dry limestone bluffs and ridges in the neighborhood of Dallas and Fort Worth, the valley of the Colorado River near Austin and similar places in Texas. The term, 'mountain ash' is more commonly used to designate *Sorbus americana* Marsh. and *S. aucuparia* L., the latter more properly called the European mountain ash or rowan tree, both insect pollinated members of the rose family and of no importance in hayfever.

Arizona ash (*F. velutina* Torr.) is a small tree scarcely over 30 feet in height, with velvety pubescent branchlets and leaves with three to five leaflets pubescent below. It is common in mountain canyons, along desert streams and borders of lakes or springs in southern Arizona, New Mexico and eastern Texas. It flowers in March or April with the unfolding of the leaves. Several varieties are recognized; the desert or leatherleaf ash (*F. velutina coriacea* Rehd., *F. coriacea* Wats.) distinguished principally by its thicker and leathery leaves and less pubescent branchlets. It has a wider distribution reaching from southern Utah to southern California, and is frequently cultivated. A still more glabrous form (var. *glabra* Rehd.) is cultivated in the cities of Arizona. *F. velutina Toumeyi* Rehd. is a form with 5 to 7 lanceolate or elliptic leaflets smooth on the upper surface but pubescent below. It is sometimes regarded as a separate species (*F. Toumeyi* Britt., *F. attenuata* Jones), and is the form generally known as Arizona ash since it is commoner in Arizona than the others, and it is the one generally planted as a shade tree in the streets of towns in southern Arizona. It is, however, less common in New Mexico.

Oregon ash (*F. oregona* Nutt.) is a fairly large tree reaching 80 feet in height with a narrow upright head or broad shapely crown, usually in rich moist soil in the neighborhood of streams in the coastal region from British

Columbia to the San Francisco Bay region of California, and in the western foothills of the mountains of San Bernardino and San Diego Counties. It flowers in April and May with the unfolding of the leaves, and is regarded as one of the most important causes of hayfever in early spring in Oregon (CHAMBERLAIN 1927).

Plantaginaceae (The Plantain Family)

The plantain family comprises three genera and about 225 species but only those of the following genus are of interest in hayfever studies.

Plantago (The Plantains)

The plantains are low herbs, mostly stemless, the scapes arising from a rosette of basal leaves and bearing terminal spikes or heads of small inconspicuous greenish or brownish flowers. Calyx and corolla are both present, generally four parted, minute and inconspicuous. One species, *P. Psyllium*, native of India furnishes the valuable psyllium seed. A case of allergy to this has recently been reported (ASCHER 1941). The patient was a pharmaceutical worker, affected by the ground seeds with which he worked.

The pollen grains (fig. 51H) are spheroidal, 16 to 40 μ in diameter, without furrows but provided with 4 to 14 pores which are circular or irregular in outline and variously scattered, their membranes flecked or provided with a single central thickening. The exine is always thin and more or less rough granular or mottled. In these characters there is considerable variation among the different species so that the grains of the common species can generally be easily told apart.

The genus comprises about 200 species of wide distribution. Of these about 20 are native or naturalized in North America. Apparently all are entirely wind pollinated but only the English plantain (*P. lanceolata* L., fig. 56) sheds enough pollen and is itself abundant enough to cause hayfever. It is a low herbaceous weed producing a basal rosette of prominently ribbed leaves from which arise the straight or nodding flowering scapes bearing at their summits short dense spikes of flowers. The flowers are perfect, first functioning as female then as male; as anthesis progresses from the base to the tip of the spike, the upper flowers of the spike, while still unopened, may be seen to protrude their single unbranched filiform styles exposing their longitudinally stigmatic surface to receive pollen, while the flowers below are seen to have opened and lost their styles, instead having four stamens, their anthers protruding far out on slender filaments and scattering their pollen which is blown freely away by the wind.

English plantain begins to flower in April or early in May and continues throughout the summer, but the bulk of its flowering takes place in May and June, a period almost coinciding with the worst of the grass hayfever season. It is native of Europe and Asia but naturalized in fields and waste places almost throughout North America, and is undoubtedly an important cause of hayfever, though in no way comparable in this respect with the

grasses with which it is generally associated. BERNTON (1925) states that 4.3 per cent of a series of hayfever cases in the District of Columbia reacted to its pollen, and BLUMSTEIN and TUFT (1937) report that 17.5 per cent of the early summer hayfever cases in the Philadelphia area were sensitive to plantain pollen.



FIG. 56. — English plantain (*Plantago lanceolata*), plant in flower.

The pollen grains of the English plantain are enormously various in size, ranging from about 25 to 40 μ in diameter. They may always be distinguished from those of the common plantain by their germ pores which are 7 to 14 in number, almost circular in outline, encircled by a thickened rim and

with their membranes provided with a single central thickening, each pore thus resembling the single pore of the grains of the grasses.

Of the other species growing in America the two which are most commonly distributed are Rugel's plantain (*P. Rugelii* Dcne.) and the common or greater plantain (*P. major* L.). Rugel's plantain is probably native of America while the common plantain is probably introduced from Europe. Now, however, both are practically universally distributed in fields and waste places throughout most of the world. The two species are very much alike and obviously closely related. Both have long-petioled coarse ovate leaves forming a basal rosette and long cylindric spikes of inconspicuous greenish flowers. But they may be distinguished from each other by certain technical details of their seed capsules, also by the fact that the leaves of Rugel's plantain are generally shining above while those of common plantain are generally dull, and the flowering spikes of Rugel's are generally much less dense than those of the common plantain. Both species flower almost throughout the summer but they shed so little pollen that, no matter how abundant the plants may be, it can never be considered a factor in hayfever. BLUMSTEIN and TUFT (1937), however, have shown that the pollen of common plantain contains the same antigenic factor as that of English plantain.

The pollen grains of both Rugel's and common plantain are occasionally caught on pollen slides but are easily distinguished from those of English plantain, and perhaps more readily from each other than are the plants themselves. Those of Rugel's plantain are 22 to 24 μ in diameter with 6 to 10 germ pores of irregular shape and size not surrounded by a thickened rim and with their membranes flecked with several small granules. The exine is thick and generally more coarsely granular than that of the grains of English plantain, or even mottled. The grains of common plantain are smaller, 16 to 21 μ in diameter, with only 4 to 6 germ pores. These, as in the grains of Rugel's plantain, are irregular in size and shape, without thickened rim and with their membranes flecked with several small granules, but their exine is even more coarsely granular and mottled.

The other species of plantain found in America are generally not weeds of waste places and are rarely abundant enough to deserve consideration as possible causes of hayfever.

Compositae (The Composite or Sunflower Family)

The composite family is distinguished from all others by having the flowers, generally more than one, assembled on a common receptacle and surrounded by one or more rows of involucre bracts (fig. 57). The result of this arrangement is that the heads of flowers present the appearance of being individual flowers. Indeed, by early botanists they were so regarded, and this conception still survives to a certain extent in the terminology used with these flowers. Botanists of today are careful to explain to the uninitiated that a daisy, a sunflower or a chrysanthemum is not really a flower but an assemblage of a large number of little flowers on the expanded end of a flower stalk, and that the white or colored structures which, if the varieties are single, radiate from the margin like petals, are not petals, but each a specially modified little flower with a strap-shaped corolla. Still the stalk which supports the assemblage of flowers is called the peduncle and its expanded end which bears the little flowers, the receptacle, the same terms which are applied to the stalk and its expanded end which bears the parts of the flower in speaking of single flowers of other families. And the inflorescence of the *Compositae* is spoken of as being paniculate, corymbose, cymose, etc. whereas by definition in the *Compositae* it is really always capitate; the terms which in other families are used to describe the arrange-

ments of flowers on their stalks are here used to describe the arrangements of heads of flowers. In studying the *Compositae*, therefore, one must often speak of the flower heads as though they were individual flowers while bearing in mind that they are assemblages of little flowers. But one must not speak of the ray flowers as petals nor of the involucre bracts as sepals, for this does not have the sanction of botanical usage.

Not only does the composite flower head look like a single flower but in some ways it functions as such. The ray flowers which in many cases look

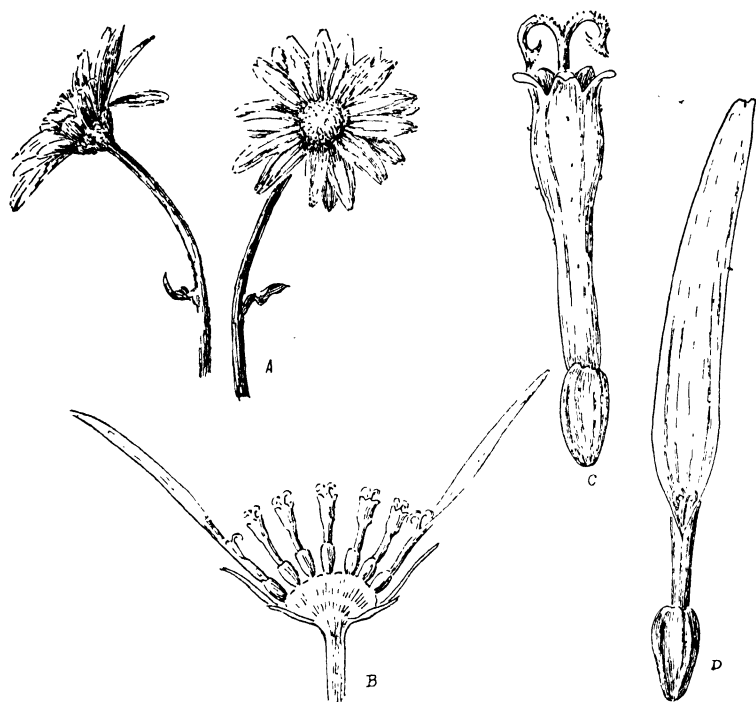


FIG. 57.— Composite flowers: A, Two flower heads; B, Section of flower head, diagrammatic; C, Disk flower; D, Ray flower.

very much like petals often have no other function than attractiveness, being quite sterile and producing neither seeds nor pollen. Among the wind pollinated members of the family these are always absent, and among the ragweeds which are monoecious, the pistillate heads are one flowered and the involucre bracts fused, enveloping the single flower as a calyx tube of individual flowers often does in other plant families.

"The *Compositae* are at once the largest, the most distinct, and the most uniform, and therefore the most natural of all orders of *Phenogamous* [flowering] plants". With these words GEORGE BENTHAM (1873) opens

his memorable essay, Notes on the Classification, History and Geographical Distribution of the *Compositae*. BENTHAM also says, "I cannot recall a

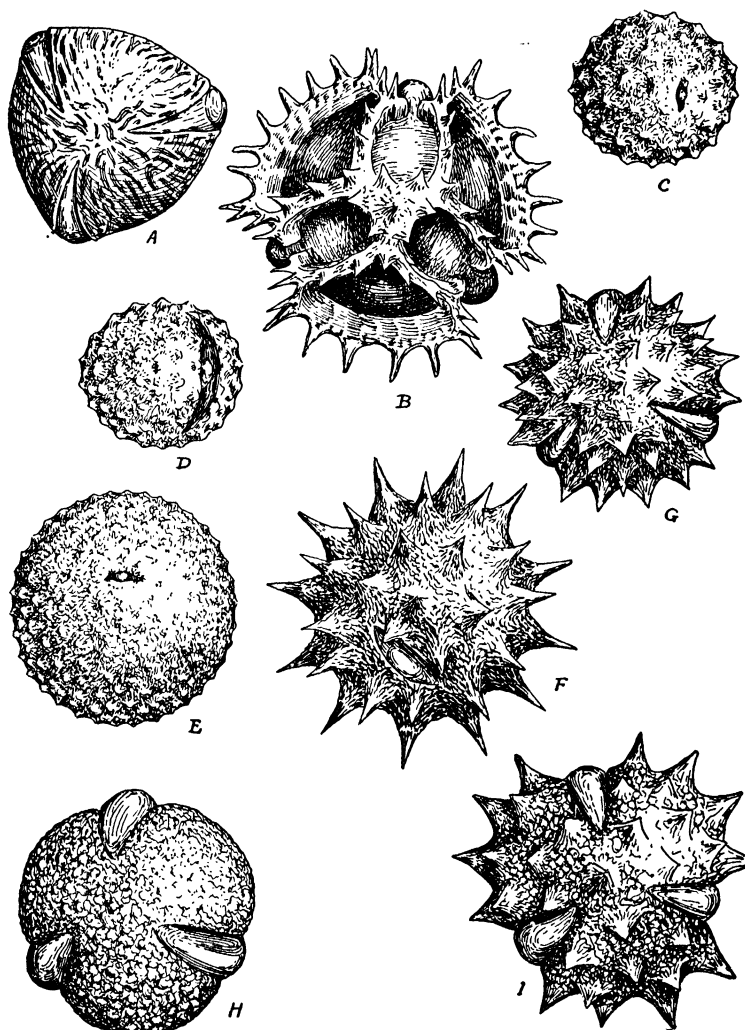


FIG. 58. — POLLEN GRAINS OF QUASSIA AND COMPOSITE FAMILIES: A, Tree-of-heaven (*Ailanthus*); B, Dandelion (*Taraxacum*); C, Short ragweed (*Ambrosia elatior*); D, Prairie ragweed (*Cyclachaena xanthifolia*); E, Cocklebur (*Xanthium speciosum*); F, Sunflower (*Helianthus*); G, Goldenrod (*Solidago*); H, Sagebrush (*Artemisia tridentata*); I, *Chrysanthemum*. All magnified 1300 times.

single ambiguous species as to which there can be any hesitation in pronouncing whether it does or does not belong to the order". When this was

written about 10,000 species were known. Though this number has since risen to over 30,000 (SMALL 1917-1919), these words are no less true today than they were 71 years ago. The family, though the largest of the flowering plants, is compact and stands apart without known connections with any other group.

Pollen Grains: — The pollen grains of the *Compositae* are extremely various (fig. 58). Nevertheless, all the different forms are the result of modifications of a certain basic form which, with little variation, characterizes by far the majority of the species. This basic form may be described as of medium size, spheroidal or slightly oblate when expanded, ellipsoidal when dry, with a thick granular exine with conical spines, thin intine, and provided with three meridionally arranged furrows which permit the emergence of the pollen tube or tubes at time of germination, and permit, by opening and closing, considerable expansion and contraction of the grain without rupturing its walls. Unmodified this form is found in the grains of the sunflower (fig. 58F). In these the exine is finely and faintly granular, more so at the bases of the spines. The latter are long and sharp pointed and can be seen to consist of two parts, a swollen granular base from which arises a slender homogeneous shaft tapering to a fine sharp point. The three furrows are only moderately long and when the grain is expanded each is seen to be crossed by a delicate elastic membrane which bears at its center a clearly defined germ pore, through which the germinal papilla, the pollen tube *Anlage*, may bulge more or less prominently. When the grain dries and assumes its elongate form the furrows close up tightly, becoming converted to shallow longitudinal grooves.

The grains of the majority of *Compositae* have well developed spines, though their size and shape vary from tribe to tribe. But in the anemophilous species the spines are greatly reduced (*e.g.*, the ragweeds and cockleburrs) or entirely absent (*e.g.*, some mugworts and sagebrushes). Another modification is for the exine to be thrown into an elaborate system of anastomosing ridges, bearing spines on their crests (*e.g.*, the chicory and ironweed tribes), or without spines (*e.g.*, *Barnadesia*). The furrows also vary greatly in length; in some they are very long, almost reaching the poles (*e.g.*, prairie ragweed) or they may be reduced to minute pits almost coinciding in extent with their enclosed germ pores (*e.g.*, ragweed and marshelder). In spite of their wide variation, however, the grains of the *Compositae* are always quite characteristic and easily recognized when encountered.

Classification: — The huge number of species included in the *Compositae* have been variously arranged by different authors, but as treated today they are generally grouped into 14 tribes. The interrelationships of the tribes, as suggested by their arrangement below, are those of BESSEY (1915) modified by SMALL (1917-1919). BESSEY gave each of the tribes the rank of family, a procedure which as far as I know has not been followed by any later investigator. It should be noticed, however, that some botanists

treat some of the tribes as separate families while leaving others. For example BRITTON and BROWN (1913), JOHN K. SMALL (1923) and PAYER (1860) regard the chicory and ambrosia tribes as separate families, designating them as *Cichoriaceae* and *Ambrosiaceae*, "A curious atavistic return to the early 18th century" (SMALL, *l.c.*). It is true that the chicory tribe is the most distinct and easily recognized of the 14 tribes, but the distinctions are scarcely important enough by ordinary botanical standards to warrant the separation of the group from the family. Its degree of distinctness is quite fairly expressed in GRAY's Manual by giving it what amounts to the status of a sub-family (Series *Liguliflorae*). On the other hand the elevation of the ragweed tribe to the rank of family is entirely without foundation. The authors who do this, as far as I am aware, give no reasons for it. But it appears to be the result of attaching far too much phylogenetic significance to the modifications which the floral structures of these plants have suffered in response to wind pollination. The phylogenetic relationship of the ragweed tribe is most fairly expressed by BENTHAM (1873) and BENTHAM and HOOKER (1873) who saw these modifications in their proper perspective, by treating the group as merely a subtribe of the sunflower tribe. The closeness in relationship of the members of the ragweed tribe to those of the sunflower tribe is of particular interest to allergists who find that ragweed hayfever patients are invariably as sensitive to sunflower pollen as to that of ragweed, though resistant to the pollen of *Compositae* of other tribes.

THE FOURTEEN TRIBES

Heliantheae, Sunflower tribe
Ambrosieae, Ragweed tribe
Helenieae, Sneezeweed tribe
Arctotideae, African daisy tribe
Calenduleae, Calendula tribe
Inuleae, Inula tribe
Astereae, Aster tribe
Vernonieae, Ironweed tribe
Eupatorieae, Boneset tribe
Anthemideae, Chamomile tribe
Senecioneae, Groundsel tribe
Cynareae, Thistle tribe
Mutisieae, Mutisia tribe
Cichorieae, Chicory tribe

Heliantheae: — The sunflower tribe is in many ways the most typical of the family and is probably the most primitive. The group is best known to us through such late flowers of the garden as the sunflower, dahlia, zinnia and cosmos, and the black-eyed-susan of the summer meadows. Their flower heads generally comprise two types of florets, the small pollen bearing flowers of the disk, and the large showy radiate flowers of the margin which look like petals. The flowers are nearly always obviously insect pollinated, though often somewhat imperfectly, so that some pollen is scattered. Owing to this latter fact and their close relationship to the ragweeds, members of this tribe should be regarded as potential hayfever plants, though restricted by the lack of buoyancy of their pollen. Sunflower, dahlia, cosmos, black-eyed-susan and others, both wild and cultivated, are known to cause

hayfever when handled by susceptible individuals, and occasionally their pollen may even become atmospheric to a small extent. In this respect the common sunflower (*Helianthus annuus* L.) is the most important. In its large headed form it is cultivated almost throughout the United States. In its small headed form, regarded by some as a separate species. (*H. lenticularis* Dougl.), it grows wild, sometimes in enormous quantity on prairies and alluvial ground almost throughout the United States west of the Mississippi River. Both forms are undoubtedly contributors to late summer hayfever. In the same category is the feverfew (*Parthenium Hysterophorus* L.). It is one of the commonest weeds of vacant lots throughout much of the South. It is similar in habit and appearance to the ragweeds and is undoubtedly closely related to them. It has occasionally been suspected of causing hayfever (SCHEPPEGRELL 1916a), but is probably of only slight importance because its pollen is "tenacious and difficult to scrape off even for microscopical observation" (KAHN 1924).

The pollen grains of the *Heliantheae* (fig. 58F) are typical of the family. They are always conspicuously echinate with spines generally long and pointed, though there is considerable variation among the members in this respect. In the pollen grains of some, particularly the feverfews and their close relatives, the spines are short and conical resembling those of the *Astereae*. The exine is moderately thick and finely and faintly granular, especially around the spines. The furrows are generally broad, of medium length, and tapering to pointed ends, each enclosing a large germ pore through which the germinal papilla may bulge prominently. The furrows are generally three in number, but may be otherwise. For example, in the grains of dahlia they are always six. The pollen grains of both the ordinary and aberrant *Heliantheae* have been made the subject of an extended investigation by the author (WODEHOUSE 1928b, 1935).

Ambrosieae: — The ragweed tribe is familiar through such well known plants as the ragweeds, cockleburrs and marshelders. All are wind pollinated, exhibiting extreme simplification of their floral structure in adaptation to this mode of pollination. The flower heads are always small and never showy, and the florets are unisexual. In some cases the staminate flowers are clustered in the center and the pistillate on the periphery of the same flower heads; in others the staminate and pistillate flowers are in separate heads but on the same plant.

CLASSIFICATION OF THE AMBROSIEAE*

IVENEAE

Oxytenia, Copperweeds

Chorisiva

Iva, Marshelders

Leuciva

Cyclachaena, Prairie ragweeds

Euphrosyne

Dicoria

* Modified from RYDBERG (1922).

AMBROSINEAE

Hymenoclea, Greasebushes*Ambrosia*, Ragweeds*Franseria*, False ragweeds*Xanthium*, Cockleburrs

This tribe is most closely related to the *Heliantheae*, merging with it through the feverfews of that tribe which bear a remarkable resemblance to the ragweeds, except that they are insect pollinated. The *Ambrosieae* should perhaps be regarded as wind pollinated derivatives of the sunflower tribe. The pollen grains of all show the typical modifications of response to wind pollination, the exine being invariably thinner and the spines shorter than in the grains of the *Heliantheae*.

Iva (The Marshelders)

The marshelders are coarse annual or perennial herbs, occasionally partly woody, generally rough, with thick opposite leaves or the upper alternate, bearing small nodding axillary and solitary, spicate-racemose, or

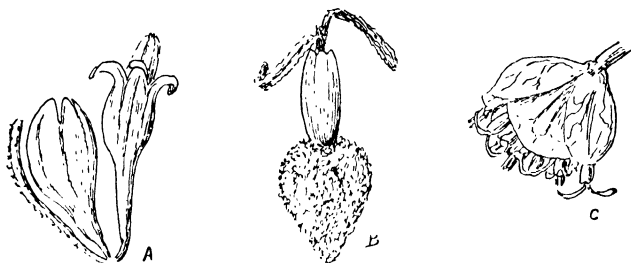


FIG. 59. — Marshelder (*Iva*) flowers. A, disk; B, marginal, both greatly enlarged; C, flower head, less enlarged.

paniculate heads of greenish flowers (fig. 59) in the axils of leaf like bracts, the staminate in the center of the head with one to six pistillate around the margin. All species are entirely wind pollinated, sometimes shedding large quantities of pollen which interreacts more or less perfectly with that of the ragweeds (PRINCE and SECREST 1939) and is known to cause hayfever in regions where they are abundant.

Their pollen grains are scarcely distinguishable from those of *Ambrosia*. They are 19 to 21 μ in diameter and with spines generally slightly less prominent than in the grains of *Ambrosia*.

The genus comprises about 11 species native of North America. All are potential causes of hayfever on account of their mode of pollination, the amount of pollen they shed, and its apparently universal character of allergenic toxicity, but only three species can actually be regarded as important factors in hayfever.

Common marshelder or high-water shrub (*I. oraria* Bart.) is a herbaceous or partly shrubby perennial, abundant in tidal marshes along the

Atlantic and Gulf coasts from Massachusetts to Texas. In the southern part of its range (south of Virginia) the plants assume a slightly different form from those of the northern part, differing in their somewhat narrower leaves and slightly smaller flower heads, and are generally known as *I. frutescens* L. The difference between the two forms, however, is scarcely



FIG. 60. — Rough marshelder (*Iva ciliata*).

enough to be regarded as specific, and for all practical purposes the two names should be regarded as synonymous. The plants flower from July to September, beginning and ending their flowering period two or three weeks earlier than the ragweeds in the same regions. On account of its restricted range and general lack of abundance this species is only a local and occasional cause of hayfever.

Rough marshelder (*I. ciliata* Willd., fig. 60) is a coarse hispid annual with the aspect of ragweed but less branched, about 2 to 6 feet high and with its flower heads in long terminal spikes. It is generally found in moist and alluvial soil from Illinois to Louisiana and westward to Nebraska and New Mexico. It flowers in August and September shedding fairly large amounts of pollen which is an important cause of hayfever.

Poverty weed or small-flowered marshelder (*I. axillaris* Pursh) is a low perennial herb, generally less than 2 feet high with a creeping rootstock, flowering from May to September. Its flower heads are small and inconspicuous in the axils of the upper leaves. Though individual plants shed only little pollen, they are frequently so numerous that they are an important factor in hayfever. They are abundant in saline soils from Saskatchewan to British Columbia and southward to New Mexico and California.

Oxytenia

Copperweed (*Oxytenia acerosa* Nutt.) is a shrubby erect perennial occurring in the alkaline plains of the Death Valley region and eastward to Arizona and Utah. It is not known to cause hayfever but the plants have been shown by SCHWARTZ and WARREN (1940) to cause dermatitis by contact. They are said also to be poisonous to stock.

The pollen grains of copperweed differ from those of ragweed in that their furrows are long and their spines well developed, resembling more closely the grains of *Parthenium* (WODEHOUSE 1935).

Cyclachaena (The Prairie Ragweeds)

The cyclachaenas are coarse annual herbs with numerous small bractless flower heads in panicles, each with 8 to 20 staminate and about 5 pistillate flowers, the latter with their corollas represented by a small hyaline ring or absent. They are easily distinguished from the marshelders with which they are often confused in hayfever literature, by their paniculate bractless inflorescence and the reduced corollas of their pistillate flowers. The genus comprises four species characteristic of prairie and arid regions of the western states and Mexico. All are entirely wind pollinated and produce large quantities of pollen of marked hayfever toxicity, but only the following species is abundant enough to be considered a factor in hayfever.

The pollen grains (fig. 58D) of all four species are alike except for slight differences in the size and distance apart of their small spines. They may easily be distinguished from the grains of *Iva* and *Ambrosia* by their exceptionally long germinal furrows which are so long that they almost meet at the poles of the grain, a character which suggests a considerable genetic gap between this genus, and *Iva* and *Ambrosia*.

Prairie ragweed (*C. xanthifolia* Fresn., fig. 61), also known as burweed, horseweed and carelessness, is a tall coarse annual reaching a height of six feet or more, with large leaves resembling those of cocklebur in their broad form and rough texture. The flower heads are small and numerous in terminal naked panicles and axillary spikes.

Prairie ragweed has much the habit of tall ragweed and, like it, is favored

by disturbed soil, and is frequently abundant in waste places in and about settled regions. Its range extends from Illinois to Saskatchewan and Idaho and southward to New Mexico, Texas and Missouri. It flowers from July to August producing enormous quantities of pollen, sometimes even out-ranking that of ragweed, with which it interreacts more or less perfectly

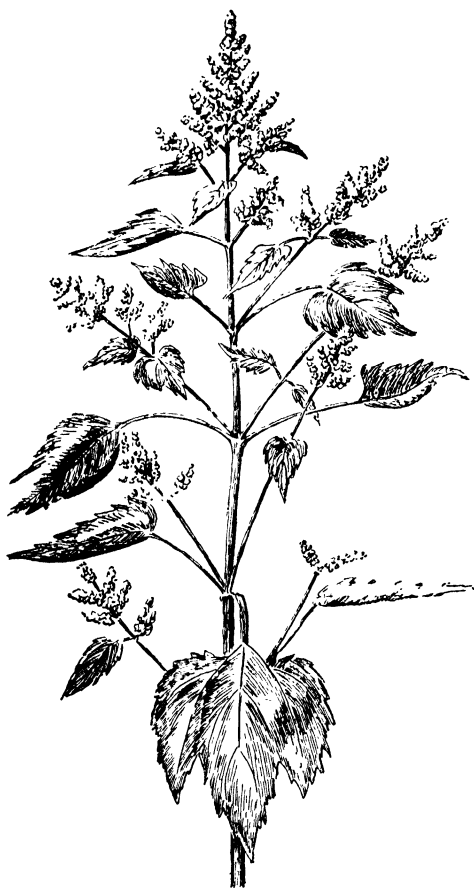


FIG. 61. — Prairie ragweed plant (*Cyclachaena xanthifolia*).

(FEINBERG and DURHAM 1933), and is one of the most important causes of hayfever throughout much of its range. Both its leaves and pollen are also known to cause dermatitis (CUNNINGHAM and WOLFE 1932, HUBER and HARSH 1932).

In hayfever literature prairie ragweed is generally known as 'burweed marshelder'. Such can only be regarded as a misnomer, probably arising

from its unfortunate assignment by some botanists to the genus *Iva* as *Iva xanthifolia* Nutt., which name is also in common usage.

Dicoria

Two species of *Dicoria* are also considered to be possible causes of hayfever in the arid regions of the Southwest. One of these, *D. canescens* Gray, is a spreading annual herb about one to three feet high, with striate stems, leaves densely white hirsute on both sides and long petioled, the lower lanceolate and dentate, the upper oval or suborbicular, the flower heads borne in numerous leafy panicles. The staminate and pistillate flowers are borne in the same heads, with the paleae subtending the latter usually large becoming more than one half inch long in fruit. The plants occur in sandy washes of Arizona, southeastern California and southern Utah, especially in the

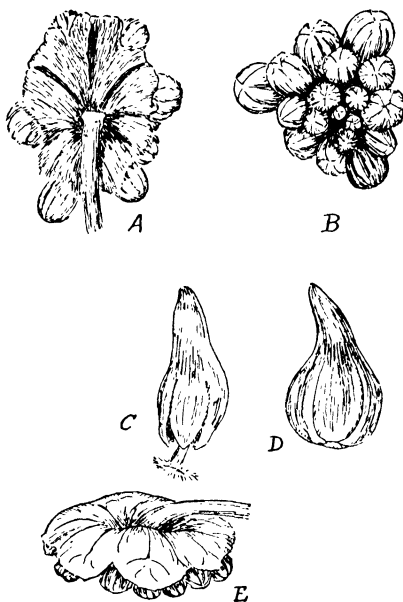


FIG. 62. — Ragweed (*Ambrosia*), staminate flower heads and florets. A, B, E, flower heads; C, floret just after shedding its pollen; D, floret unopened.

Colorado and Mohave deserts. The other, *D. Bradegei* Gray, is similar in appearance and habit but may be distinguished by the smaller size of the paleae subtending the pistillate flowers, and its oblong-lanceolate or linear leaves. Its distribution is also similar, occurring in southwestern Colorado, southern Utah and Arizona. Both species appear to have hayfever possibilities but their importance in this respect is not fully understood. They are, however, regarded by SELFRIDGE (1918) as important in hayfever.

Ambrosia (Ragweeds)

The ragweeds are coarse annual or perennial herbs with lobed or variously dissected leaves. They are distinguished from the marshelders and

prairie ragweeds by having their staminate and pistillate florets on different parts of the plant. The staminate heads are nodding in terminal spikes, their involucral bracts united, five to fifteen lobed and umbrella like above the nodding heads (fig. 62 A, B, E); the pistillate heads are borne below the staminate spikes, erect, each with but a single floret which is completely enveloped by its involucre of united bracts with only a small opening at the tip of an apical beak-like projection through which the two-branched style may protrude. The involucre of the pistillate head with its single enclosed floret is ovoid with its beak surrounded by a single series of tubercles or short spines. It is chiefly on these characters that the genus is distinguished from the remarkably similar and closely related group of the false ragweeds (*Franseria*), the involucre of the pistillate heads of the latter being provided with more than a single row of tubercles or spines.

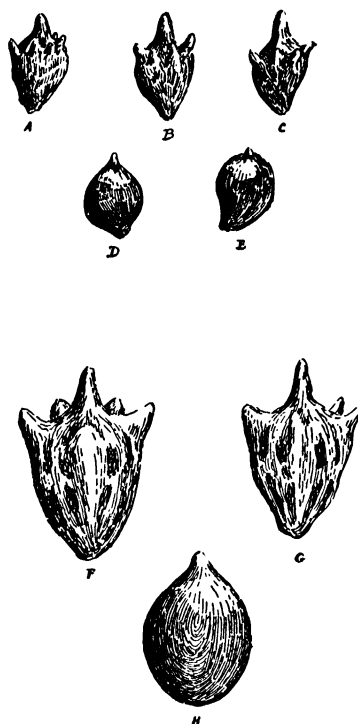


FIG. 63.—Ragweed (*Ambrosia*) seeds. A-C, short ragweed, with their outer coats still on; D, E, their outer coats removed; F, G, tall ragweed, their outer coats still on; H, its outer coat removed.

The pollen grains (fig. 58C) are oblate spheroidal, 17 to 24 μ in diameter, with small and scarcely pointed spines, somewhat various among the different species. The furrows, generally three or occasionally four or more, are short and pit like, almost coinciding in extent with their small enclosed

germ pore. The exine is moderately thick, thicker than that of the grains of *Xanthium* and most species of *Franseria*, and finely but conspicuously granular. These grains are virtually indistinguishable from those of *Hymenoclea*, *Iva*, *Acanthambrosia*, *Acanthoxanthium* and some species of *Franseria*. They are, however, easily distinguished by their short pit-like furrows from the grains of *Cyclachaena*, *Oxytenia*, *Chorisiva*, *Dicoria*, *Leuciva* and *Euphrosyne*, all of which have long tapering furrows, and by their more prominent spines from the grains of *Euxanthium* and some species of *Franseria*. Outside of the family, however, there appears to be no species with which ragweed pollen grains could be confused.

The genus comprises 21 species, all entirely wind pollinated and shedding exceptionally large quantities of buoyant pollen. The pollens of the different species appear to interreact more or less perfectly so that sensitization to that of one of them implies a greater or less sensitization to that of the others (PRINCE and SECREST 1939). However, that the antigenic structures of the pollens of the different species are not always identical has been shown by CROMWELL and MOORE (1933) in the case of the tall and short ragweeds. Though all species are potential causes of hay-fever, only the following are abundant enough to be of much importance. These appear to owe their great abundance to their extraordinary ability to take possession of freshly disturbed or denuded soils, and the longevity of their seeds which have been shown (DARLINGTON 1941) to be capable of germinating after being buried in sand for 40 years. As a consequence of this they are everywhere attendant upon the ravages of an expanding human population, especially in the partially settled districts around towns and the great cities.

The classification and nomenclature of the ragweeds followed here is that of RYDBERG (1922).

Short or common ragweed (*A. elatior* L., *A. artemisiifolia* T. & G., fig. 64) is an annual herb frequently much branched, not more than 4 feet high, with rough or somewhat hairy fern like leaves, twice pinnately cleft or the upper only once cleft. The staminate flower heads are numerous, nodding in long terminal spikes. Their umbrella-like involucre are somewhat oblique, about 3 mm. wide. The one-flowered pistillate heads are borne singly or in small clusters in the axils of the upper leaves, excepting occasional plants which are predominantly pistillate in which case they largely or entirely replace the staminate heads in the terminal spikes. The short ragweed is similar in appearance to the western ragweed but may be distinguished by its fibrous annual root (the western species possesses a perennial creeping rootstock), and by its generally twice pinnatifid leaves (those of the western species are most commonly only once pinnatifid).

The pollen grains of the short ragweed (fig. 58C) are 17.6 to 19.2μ in diameter, with short and rather blunt spines and nearly always three furrows. They may be distinguished from the grains of the giant ragweed by their slightly larger size and their smaller spines, and from those of western ragweed by their smaller size and the fact that the pollen of the latter always contains a large number of grains with four germinal furrows.

The short ragweed is found almost throughout the United States, extending in distribution from the Atlantic to the Pacific through southern Canada and as far south as southern Florida and northern California in the United States, and in Cuba. Its effective range as a hayfever plant, however, is somewhat less, reaching only as far west as Montana and western



FIG. 64. — Short ragweed (*Ambrosia elatior*), flowering branch.

Kansas. It flowers from early August to late September throughout most of its range, the exact time depending upon latitude; in the northern part of its range the plants come into flower several weeks earlier than in the southern part, except in the extreme south, the west coast of Florida, Louisiana and Cuba, where it flowers from May to September.

Short ragweed, as generally understood, is a complex and variable species consisting of a number of genotypes (K. L. JONES 1936) which under natural environmental conditions tend to segregate out. Some of these have come to the attention of taxonomists and been given specific names. One is *A. artemisiifolia* L., the form first described by LINNAEUS



FIG. 65.— Tall ragweed (*Ambrosia trifida*), flowering branch.

but, as pointed out by FERNALD and GRISCOM (1935), it is easily recognizable among the progeny of a single plant of *A. elatior*. The others are *A. diversifolia*, occurring in Washington and Wyoming, *A. media* and *A. longistylis* in the Rocky Mountain region, *A. Rugelii* and *A. glandulosa* of the southern coastal plain and *A. monophylla* of the Gulf coastal region, the

Florida keys and Cuba. Only the latter is perhaps worthy of specific recognition since it has the peculiarity of flowering off season, in May and June as much as in August and September (WODEHOUSE 1942a). Morphologically it is well within the normal range of variation of the progeny of *A. elatior*.

Tall ragweed or giant ragweed (*A. trifida* L., fig. 65) is a coarse branching annual, reaching 15 feet in height, with rough stems and leaves. The latter are broad, three or five cleft or entire on rather long petioles which are more or less winged on their margins. The staminate heads are numerous, larger than those of the short ragweed, borne in long terminal spikes. The pistillate are similar to those of the short ragweed but larger, borne in small clusters at the base of the staminate spikes in the axils of three cleft bracts.

The pollen grains of tall ragweed are similar to those of the short species but may be distinguished by their smaller size, 16.5 to 19.2 μ in diameter, and their slightly more prominent spines.

In distribution the tall ragweed extends from Quebec to North Carolina and west to Colorado and British Columbia, but its effective range as a cause of hayfever does not extend west of the Dakotas, Nebraska and Kansas. It is generally found in disturbed soil, such as along the banks of streams, on flood plains (GEDDES 1875), roadside ditches, improperly cultivated farm land and vacant lots. It flowers at about the same time as the short ragweed, but generally starting a few days earlier, and throughout most of its range the pollens of the two species, which interreact almost perfectly, act together in causing hayfever so that it is not possible to tell to which species to credit the greater responsibility. On the whole the dwarf ragweed is the more widely distributed, more universally abundant and credited with the greater toxicity, but in many regions the giant far outranks the dwarf in the number of individuals, size of the plants and amount of pollen produced.

The giant ragweed is less tolerant of drought than the short ragweed and more readily invades the moister regions. Its seed (fig. 63) is partly aquatic in that its fibrous coat is only slowly penetrated by water, permitting it to be carried great distances by rivers and streams. This explains its presence along river banks and freshly silted flood plains. FOERSTE (1882) tells of another way in which its seeds may be distributed. He states that five or six strands of ice, one and a half to three inches long become attached to the beak and protuberances of the achene and these enable the seed to be carried away by the wind. I have not seen this phenomenon, but I have not looked for it in Dayton, Ohio, where he reports its occurrence.

Western giant ragweed or Texas great ragweed (*A. aptera* DC.) is very similar and closely related to the eastern giant ragweed; in fact it is sometimes regarded as merely a variety of the former (*A. trifida texana* Scheele). It can, however, be distinguished from the eastern form by its more sturdy habit of growth, its tendency to branch higher up, its more deeply cut leaves with their petioles wingless. All of these characters are somewhat various and, while convenient in the field, are not entirely reliable. The two forms

may, however, also be distinguished by their fruits; those of the giant ragweed are slightly if at all pitted between the ridges and the latter end in short conic spines; while those of the western giant ragweed are more markedly pitted between the ridges and these end in only small tubercles or the seeds are unarmed.

The pollen grains are exactly the same as those of the eastern form.

In distribution the western giant ragweed is limited to the southwestern part of the United States from Louisiana to Arizona and adjacent Mexico. It flowers in late summer shedding quantities of pollen as great or greater than the eastern giant ragweed and in regions where abundant causes much hayfever. In hayfever studies the two species of giant ragweed are seldom distinguished from each other, both going by the name of *A. trifida*.

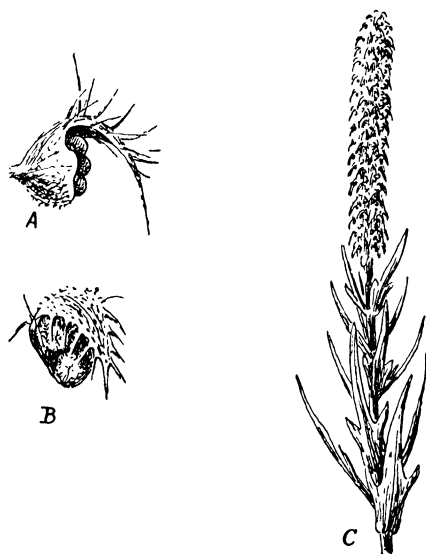


FIG. 66.— Southern ragweed (*Ambrosia bidentata*). A, B, Staminate heads; C, Flowering spike.

Southern ragweed (*A. bidentata* Michx., fig. 66), also called lance-leaved ragweed, is a rough branching annual, 1 to 3 feet high with hairy sessile leaves, generally with one large central lobe flanked by two smaller lanceolate lobes or teeth on each side. The staminate heads are numerous, sessile in dense terminal spikes, their involucre extremely oblique with a conspicuous and reflexed lanceolate lobe on the inner side. The pistillate heads are few borne singly or in clusters in the axils of the leaves below.

The pollen grains are similar to those of the giant ragweed but may be distinguished by their larger size (19.8 to 21 μ in diameter).

In distribution the southern ragweed is restricted to prairies from southern Illinois to Louisiana and westward to Texas and Nebraska, and its

effective range is further restricted, not extending west of Kansas and Oklahoma. In this area it is regarded as a local cause of hayfever from July to September but it is scarcely comparable with the other species already mentioned.

Western ragweed (*A. psilostachya* Gray) is a perennial herb with creeping rootstocks and simple erect stems, generally only 1 to 4 feet high or occasionally higher. The leaves are rough hairy mostly once pinnately divided though the lower may be twice divided. This species closely resembles the eastern short ragweed and, like it, is favored by disturbed soil. "Abandoned fields, vacant lots, roadsides and railway embankments are its usual haunts" (ABRAMS 1932). It is also often particularly abundant along irrigation ditches, but is seldom as abundant as the short ragweed in the East. In distribution it ranges from California, Idaho and Saskatchewan eastward to Illinois and Louisiana. It may flower from June to December, varying with the locality, but in most places it flowers only in September and October. It sheds large quantities of pollen which is the cause of much hayfever but on account of the more localized occurrence of the plants and their smaller size this is less important in hayfever than the pollen of the tall and short ragweeds.

The pollen grains of the western ragweed are similar to those of the eastern giant ragweed, with spines somewhat larger and more pointed than in the grains of the short ragweed. They also differ in their larger size, 22 to 24.7 μ in diameter, and in the fact that nearly half of the grains have four instead of the usual three germinal furrows. Though the pollen grains are slightly larger than those of the other species mentioned, they are still quite small enough to be carried freely in the air.

The species occurs in several slightly different forms which are regarded by some taxonomists as different species (RYDBERG 1922), as *A. coronopifolia* T. & G., *A. californica* Rydb., and *A. psilostachya* DC. For purposes of hayfever studies, however, such taxonomic refinements are neither necessary nor desirable, and these names may be treated as synonyms.

Among the remaining members of the genus several others are occasionally mentioned as possible causes of hayfever, and, indeed, it is quite possible that some of them may be local factors, but they lack the weedy habit of invading freshly denuded territory which is the chief characteristic which leads to the present abundance of those already mentioned. Among the species of secondary or doubtful importance are the seashore ragweed (*A. hispidula* Pursh), a low prostrate creeping perennial herb with white hairy leaves their blades twice pinnately cleft. It commonly occurs only on sea beaches and coastal dunes of Florida, Cuba, the Bahamas and Central America where it serves as a sand binder. It is suspected of contributing to the ragweed pollen in the air in parts of Florida (DURHAM 1933b). It flowers almost throughout the year but appears to be of little or no consequence in hayfever, probably because of its local distribution, also because it is still growing in normal balanced relation to its environment, uninfluenced by human activity.

Another species which is sometimes mentioned in hayfever literature is the dwarf or Tiajuana ragweed (*A. pumila* Gray). It is a low and inconspicuous weed with small finely dissected grayish leaves. According to ABRAMS (1932), "It inhabits lower California and reaches its northern limit in southern San Diego County, California, where it may be a local factor".

Franseria (False Ragweeds)

The false ragweeds are similar and closely related to the true ragweeds and to the cockleburs, constituting a chain of connecting links between these two genera. Their chief distinguishing characters are found in the involucre of the pistillate heads; these, instead of having only a single circle of tubercles or spines as in the ragweeds, are provided with several series, the fruits developing into a bur at maturity, in some cases similar to that of the cockleburs. In some species the pistillate heads are one flowered and one beaked, as in the ragweeds (fig. 69), in others they have a larger number of flowers and a correspondingly larger number of beaks up to eight, even more than the cockleburs.

The pollen grains of most species are similar to those of the ragweeds, while those of others have only vestigial spines like those of most cockleburs.

The genus comprises about 39 species of annual or perennial herbs or low shrubs, principally of western distribution. Though they have the same hayfever proclivities as ragweeds and their pollen interreacts with that of the ragweeds more or less perfectly, they are much less important in hayfever because they are less common and less widely distributed.

Bur ragweed (*F. acanthicarpa* Cov., *Gaertneria acanthicarpa* Britt., fig. 69) is a diffusely branching hirsute annual generally with stems 1 to 2 feet high, similar in appearance to short ragweed. The staminate heads are loosely arranged in numerous paniculate racemes, the pistillate heads one flowered in small clusters in the upper axils. These at maturity are armed with numerous long flat straight spines.

The pollen grains are 18.7 to 20.3μ in diameter similar to those of short ragweed but with their spines slightly less prominent.

Bur ragweed is a natural inhabitant of sandy plains and valleys and summer beds of winter flood streams. It is also specially common in cultivated and waste grounds throughout the United States principally west of the Mississippi River and adjoining parts of Canada, and in many places is the commonest weed of cultivated fields. It flowers from July to October shedding large amounts of pollen which in many parts of its range is one of the worst causes of hayfever. On account of its spiny fruits and preference for sandy soils it is sometimes called sandbur.

Slender ragweed (*F. tenuifolia* Harv. & Gray, *Gaertneria tenuifolia* Ktze., fig. 67) is an erect perennial herb closely resembling western ragweed, 1 to 2 feet high with rough stems and leaves, the latter interruptedly bi- or tri-pinnatifid with the divisions narrow, the terminal one often elongate. The staminate heads are about 3 mm broad, their involucre dark brown with three blackish ribs, loosely arranged in narrow paniculate spikes. The pistillate heads are borne in small clusters in the upper leaf axils 1 or 2 flowered, developing at maturity into a bur with stout hooked spines.

The pollen grains are similar to those of the giant ragweed but somewhat larger, 19.8 to 20μ in diameter.

Slender ragweed "grows in warm dry districts from the westerly part of the Mississippi Valley to Colorado, Nevada and southern California, and

ranges south to Texas" (HALL in SCHEPPEGRELL 1917 a). It flowers from July to October shedding fairly large amounts of pollen. Throughout most of its range it appears to be much less important than other members of the ragweed tribe, but in parts of Arizona it is counted among the most important causes of hayfever and is rapidly becoming more so (PHILLIPS 1928-1930).



FIG. 67. — Slender ragweed (*Franseria tenuifolia*), part of a flowering plant.

Canyon ragweed, rabbit bush, Arizona bur sage (*F. deltoidea* Torr., *Gaertneria deltoidea* Ktze.) is a shrubby perennial with finely tomentose branches, of arid regions in southern Arizona and Mexico. It flowers in early spring, and is reported by ABRAMS (1932), WATSON and KIBLER (1922) and PHILLIPS (1932) as an important cause of hayfever in Arizona.

Its pollen grains are similar to those of cocklebur with vestigial spines, 20 to 22 μ in diameter.

The desert bur sage, burrow weed or sand bur (*F. dumosa* Gray, *Gaertneria dumosa* Ktze.) is a low grayish shrub, not more than 20 inches high with rigid branches terminating in spicate inflorescences which become in the second year naked hardened spines. It grows in great abundance in the Colorado and Mohave deserts, its range extending eastward to Utah and southward into Mexico. It flowers from about March 10 to June when the hot weather begins, and is known to be a severe cause of hayfever in Arizona (PHILLIPS 1932).

Sonora bur sage or canyon ragweed (*F. ambrosioides* Cav.) is a shrubby perennial with large spiny burs and broad petioled leaves, with something of the appearance of a cocklebur, occurring in desert areas of Arizona, Mexico and Lower California. It flowers from March to May, and is regarded as important in hayfever (ABRAMS 1932, PHILLIPS 1932).

Among the remaining species of *Franseria* several are regarded as possible causes of hayfever but at their worst they could only be local contributors on account of their lack of abundance and restricted distribution. Such a one is the low ragweed (*F. discolor* Nutt.). It is a low perennial herb with creeping rootstock, irregularly bipinnatifid leaves, white tomentose beneath. It occurs on plains from South Dakota and Nebraska to New Mexico, Arizona and Wyoming. Another is the beach sandbur (*F. bipinnatifida* Nutt.). It is a low spreading perennial herb with leaves twice or thrice pinnatifid and long prostrate running stems with their ends turning abruptly upward and ending in a spike of staminate flower heads. It is common on sea beaches and sand dunes where it acts as a sand binder, from Lower California to British Columbia. It flowers from April to December, and is reported to be an important local cause of hayfever (ROWE 1928). Often associated with it is the less common but similar and closely related false ragweed (*F. Chamissonis* Less.). This may be distinguished from the preceding species by its leaves which are merely serrate or the lower incised.

Xanthium (The Cockleburs)

The cockleburs are coarse annual weeds with widely branching stout stems and petioled lobed leaves (fig. 68). The flower heads are unisexual; the staminate greenish, subglobose, with involucre of slender and entirely separate bracts, arranged in terminal spikes above the pistillate heads, the latter two flowered, occasionally one or three flowered, with united and closed involucre tipped by as many beaks as there are flowers and maturing into one to three seeded stout indurated burs, copiously armed with hooked spines.

The genus comprises about 20 species of world wide distribution but mostly American. These fall naturally into two sharply distinguished sections, *Euxanthium* and *Acanthoxanthium*, those of the latter distinguished by conspicuous tripartite spines borne on the stem at the base of the leaves. Such spines are lacking in all species of *Euxanthium* (MILLSPAUGH and SHERFF 1922).

The pollen grains of *Euxanthium* section (fig. 58E) are spheroidal about 22.1 to 29.1 μ in diameter with spine vestiges generally scarcely apparent, 2 to 2.8 μ apart. Their furrows are generally three, very short, merely pits in the exine; the latter is thin and finely granular. The grains of the species

of the *Acanthoxanthium* section are essentially the same as those of short ragweed, 19 to 22 μ in diameter and with low spines, 3.4 to 5.1 μ apart. In some classifications the two sections are regarded as separate genera; the great difference in the appearance of the plants and their pollen grains suggest that there is ample justification for this separation.

The cockleburrs are mostly weeds of waste places, roadsides, neglected farms and railroad embankments where they often grow in great profusion, but most species shed so little pollen that they are relatively unimportant



FIG. 68. — Cocklebur (*Xanthium*), plant and seeds.

in hayfever even where the plants are abundant. Exceptional in this respect is the great clotbur (*X. speciosum* Kearney). It is a large robust and exceedingly coarse and bushy plant, 3 to 4½ feet high with burs 1 inch long or more, provided with numerous curved prickles, themselves spiny, and two long hooked beaks. This species is common in waste ground especially where moist, throughout the Great Plains region and Mississippi Valley. It flowers in August and September and appears to shed much more pollen than most other species.

Of the other species of this genus the commonest and most widely distributed is the Pennsylvania cocklebur or clotbur (*X. pennsylvanicum*

Walr.) a similar but less robust species. It is common in waste places practically throughout the United States and parts of Canada and Mexico. This species is frequently encountered in the literature under the name *X. canadense* Mill., which is a misnomer. Undoubtedly other species are involved in hayfever but they are seldom differentiated. Indeed it appears unnecessary to differentiate them as far as concerns the members of the *Euxanthium* section of the genus, for the pollens of the various species appear to interreact perfectly with each other, and almost perfectly with those of the ragweeds (FEINBERG and DURHAM 1933). The California spiny or thorny clotbur or clotweed (*X. spinosum* L.) is the only member of the *Acanthoxanthium* section of the genus found in America. It is erect spreading much branched, 1 to 3 feet high with numerous pointed leaves dark green above and white canescent below. The stem is armed with sharp tripartite spines. It is naturalized from Portugal, almost throughout the United States but apparently only in California is it abundant enough

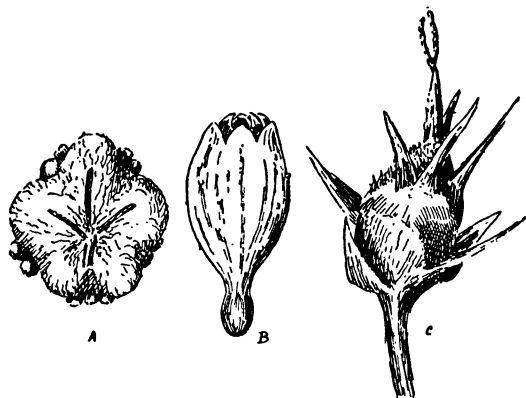


FIG. 69.— Bur ragweed (*Franseria acanthicarpa*). A, Staminate head; B, Staminate floret; C, Pistillate head with the style branches of its single floret protruding.

to be a factor in hayfever. Even there it is probably unimportant, for the plants yield pollen only sparingly. It flowers from August to November.

Hymenoclea (Greasebushes)

Of less importance in hayfever are the greasebushes, *H. Salsola* T. & G. and *H. monogyra* T. & G. These are desert shrubs with narrow linear leaves, with flowers and inflorescences quite like those of the ragweeds, but the involucre of the pistillate heads have 6 to 12 dilated scarious blade like transverse wings. The former species, which is known as burrowed or romerillo is found in saline soils in Arizona and adjoining parts of Utah, Nevada and California. It flowers in spring, and is regarded as important in parts of California and Arizona (SELFRIDGE 1918, ABRAMS 1932, PHILLIPS 1932). The latter, known as Jecote, is found from California and

Nevada to eastern Texas. It flowers in late summer and is regarded as of secondary importance in Arizona (WATSON and KIBLER 1922).

Helenieae:— The sneezeweed tribe is a small group of plants similar and closely related to the *Heliantheae*. It is best known to us through such garden flowers as the marigolds (*Tagetes*), gaillardias and sneezeweed (*Helenium*), the latter occasionally suspected of causing hayfever. The odor of marigolds (*Tagetes*) has recently been stated to cause hayfever symptoms even in the absence of pollen (BIEDERMAN 1937).

Arctotideae:— The African daisy tribe is almost entirely South African, known only in America through a few cultivated forms like the African daisy (*Arctotis grandis* Thunb.) which closely resembles the ox-eye daisy except that the florets of the disk are blue.

Calenduleae:— The calendula tribe is the smallest and most compact of the family with about 100 species in 8 genera, almost entirely South African. It is best known in America through the Cape marigolds (*Dimorphotheca*) from South Africa and the calendula or pot marigold (*Calendula officinalis* L.), a common flower-garden annual from the Mediterranean region. It is improbable that any of these could be of any importance in hayfever.

Inuleae:— The inula tribe is familiar to us through such forms as the everlastings (*Antennaria*, *Gnaphalium* and *Anaphilis*) and the straw flower (*Helichrysum*).

It is unlikely that any of them could ever be of any importance in hayfever for they are entirely insect pollinated and shed but little pollen.

Astereae:— The aster tribe comprises over 1400 species distributed in about 90 genera which are so closely related to each other that it is difficult to draw their limits. The tribe is familiar to us through such forms as the asters, goldenrods, fleabanes (*Erigeron*), cultivated asters (*Callistephus*) and English daisy (*Bellis*). Though most of them appear to be entirely insect pollinated, some shed much more pollen than is carried off by insects, and this may become a menace to hayfever sufferers from handling the plants. Or even the pollen may occasionally become atmospheric to a small degree; such is known to be the case with some of the goldenrods and fleabanes. Those who have attempted to collect goldenrod pollen have often been convinced by the meagreness of the results that goldenrods shed too little pollen to be important in hayfever. For most species this is quite true. Of sixteen species which were tested for their pollen yield, only two, the noble goldenrod (*Solidago speciosa* Nutt.) and the seaside goldenrod (*S. sempervirens* L.) could be made to yield pollen in collectable quantities. The yields from these two are quite generous. Furthermore, their pollen can often be detected in the air several miles from the fields when the plants are in flower.

In *Baccharis* the flowers are dioecious and appear to be at least partly wind pollinated. The species of this genus are mostly South American, several are found in North America, and one, the groundsel bush (*B. halimifolia* L.) is common wild and occasionally cultivated in the United States. It occurs naturally along sea beaches and in salt marshes from Florida to Texas and less abundantly along the Atlantic coast as far north as Massachusetts. It is probably a local cause of hayfever. Indeed it is reported as such in parts of Florida (NICHOL and DURHAM 1931). It flowers in the late summer at about the same time as or later than the ragweeds.

The pollen grains of the aster tribe are extremely uniform throughout the group, so much so that it is generally impossible to tell those of one

genus from those of another (fig. 58G). They are 16 to 32 μ in diameter, with finely granular exine, and provided with low conical spines. The furrows are long and tapering, each with a germ pore. Though characteristically three in number throughout the group, there is a marked tendency towards furrow proliferation. These grains with supernumerary furrows have been made the subject of extended studies by the author (WODEHOUSE 1930, 1935).

Vernonieae:— The members of the ironweed tribe are characterized by having the florets all perfect and tubular, those of the margin of their heads rarely differing noticeably from those of the center. The tribe comprises the huge genus of ironweeds (*Vernonia*) with more than 500 species, principally South American (GLEASON 1923*a, b*), and about 25 smaller genera which are scarcely represented in the United States outside of cultivation (GLEASON 1922). The best known example is Stokes' aster (*Stokesia laevis* Greene), a beautiful garden perennial with large heads of sky-blue or white flowers in summer. All are insect pollinated and their pollen sticky, so that none could possibly be regarded as a cause of hayfever, though the ironweeds have occasionally been mentioned in hayfever literature.

The pollen grains of the *Vernonieae* are unlike those of most *Compositae*; the exine is thrown into vertical spine-topped ridges describing elaborate and characteristic patterns over the surface as in the grains of the *Cichorieae*, except that their patterns are more complex. These grains have been made the subject of investigation by the author (WODEHOUSE 1928*a*).

Eupatorieae:— The boneset tribe is a distinct group of closely related forms, with heads of florets all alike, perfect and tubular. They are best known to us through the purple joe-pye-weed (*Eupatorium purpureum* L.) so conspicuous an ornament of late summer woods and meadows, the common thoroughwort or boneset (*E. perfoliatum* L.) and the blazing stars (*Liatris* or *Lacinaria*). Stevia (*Piqueria trinervia* Cav.) with its minute delicate white flower heads is used by every florist to enhance the beauty of other flowers in assembling bouquets. This plant has been shown to occasionally cause hayfever among florists and greenhouse workers. Such a case is reported by LANGLEY (1937). Their pollen grains are typical of the family, generally small, ranging from about 14 to 25 μ in diameter, with three meridionally arranged furrows long and tapering to pointed ends. Their spines, however, are always small, generally smaller even than those of the grains of the asters and goldenrods.

Anthemideae:— The mayweed tribe is a group of about 650 species in 40 genera. Most are insect pollinated and of little consequence in hayfever. Others are wind pollinated and of the utmost importance. The former are best known to us through such forms as the garden chrysanthemums, ox-eye daisy (*Chrysanthemum Leucanthemum* L.), the chamomiles (*Anthemis*),

yarrow (*Achillea Millifolium* L.), tansy (*Tanacetum vulgare* L., fig. 70A) and pyrethrum. The latter, as occurring in insecticides, is occasionally a severe cause of hayfever and asthma. These reactions are believed to be independent of the insecticidal part of pyrethrum powder which consists of complicated esters (RAMIREZ 1930). Pyrethrum powders have also been shown to cause dermatitis (SULZBERGER and WEINBERG 1930), likewise the leaves of common tansy (GREENHOUSE and SULZBERGER 1933) and of chrysanthemum (GOLDSTEIN 1931). The pollen grains of the entomophilous members of the tribe are typical of the family, characterized by their thick and coarsely granular exine, provided with broad short conical spines (fig.



FIG. 70. — Tansy (*Tanacetum*) (left) and *Artemisia*. Comparison of entomophilous and anemophilous flowers which are closely related.

58 I). The furrows are generally three, of medium length and tapering to pointed ends.

The wind pollinated members comprise the genus of mugworts, sagebrushes and wormwoods (*Artemisia*, fig. 70B) and several smaller related genera. Some of these are our worst hayfever plants, described below. Among the pollen grains of the wind pollinated members (e.g. *Artemisia*, fig. 58H), the spines are greatly reduced or entirely absent and the exine much thinner, but always with its distinctive coarse granular character.

Artemisia (Sagebrushes, Mugworts and Wormwoods)

The artemisias are annual or perennial herbs, or shrubs, usually aromatic and bitter, the annual species generally with a deep tap root and the perennial with rootstocks or woody base. The leaves are alternate in arrangement and enormously various in the different species. The flower heads (fig. 71) are small, nodding or erect in panicles or raceme like spikes, the marginal flowers (reduced rays) pistillate and fertile or absent, the disk flowers bearing both stamens and pistil or only stamens.

All species are entirely wind pollinated and most of them copious pollen shedders. Next to the ragweeds, and possibly the grasses, they constitute the most important group of hayfever plants.

Many species are extremely variable so that the dividing lines drawn between them are often arbitrary, and the group presents taxonomic difficulties not encountered elsewhere among hayfever plants. Fortunately, however, the American species have been exhaustively studied and reported on in two great taxonomic works (RYDBERG 1916, HALL and CLEMENTS 1923). The authors of these take diametrically opposite views as to the limitation of species. RYDBERG recognizes 120 species, after eliminating five which he transfers to other genera, while HALL and CLEMENTS recognize only 29, including the five rejected by RYDBERG. In RYDBERG's work virtually all forms which have ever had names attached to them are given specific rank, however slight the differences between them may be, while in HALL and CLEMENTS' work a large proportion of these have been reduced to subspecies or regarded as varieties, minor variations or synonyms of the few quite definitely delimited species. This latter treatment is the more suitable to hayfever studies because the allergenic differences between the pollen of even the most distinct species appear to be slight or negligible. Moreover the work of HALL and CLEMENTS in its clarity, consistency and completeness is perhaps the most perfect example of taxonomic work produced in modern times. So, in this discussion I have largely followed their work. In nomenclature, however, I have given preference to the names which are most commonly encountered in hayfever literature, but always with the equivalents of HALL and CLEMENTS when these are different. In this way I have recognized as species a number of different forms which by HALL and CLEMENTS are accorded only the rank of subspecies or varieties. This is a concession to custom. For example, the four species, *Artemisia campestris*, *A. caudata*, *A. canadensis* and *A. pycnocephala* are so much alike in their essential characteristics and so closely related that HALL and CLEMENTS regard them as subspecies of *A. campestris*, and it is practically certain that there are no observable allergenic differences between their pollens, so they had much better be regarded as merely varieties of one species. Still all have appeared in hayfever literature as separate species under the above names. So, rather than go against the trend and risk greater confusion than already exists, I have so treated them. Their interrelationships, together with their relationships to the other species of the genus

under the broader specific conception, however, are clearly brought out by the summary of species below.

The artemisias are probably to be regarded as wind pollinated derivatives of the tansies. There are few constant characters, except those obviously due to anemophily, by which the two genera may be distinguished.

The pollen grains of *Artemisia* are oblatly spheroidal, 17.5 to 28.5 μ in diameter, provided with normally three furrows which are long and tapering to pointed ends, their margins sharply defined, their membranes smooth and each provided with a well marked central pore. Their exine is thick and of the same peculiar coarse granular texture which is found in the grains of other *Anthemideae*, but the spines are represented by only the merest vestiges or are entirely absent. The grains of all members of the genus are essentially alike except for slight variations in their size and the prominence of their spine vestiges when present. These differences, however, are too slight to be conveniently used in their identification. This matter is discussed at greater length elsewhere (WODEHOUSE 1926, 1935).

PRINCIPAL HAYFEVER SPECIES OF ARTEMISIA

<i>A. Abrotanum</i> L.		
<i>A. californica</i> Less. (<i>Crossostephium californicum</i> Rydb.)		
<i>A. vulgaris</i> L. (<i>A. vulgaris typica</i> H. & C.)	} <i>A. vulgaris</i>	} <i>Abrotanum</i> section
<i>A. heterophylla</i> Nutt. (<i>A. vulgaris heterophylla</i> H. & C.)		
<i>A. ludoviciana</i> Nutt. (<i>A. vulgaris ludoviciana</i> H. & C.)		
<i>A. gnaphalodes</i> Nutt. (<i>A. vulgaris gnaphalodes</i> H. & C.)		
<i>A. serrata</i> Nutt. (<i>A. vulgaris serrata</i> H. & C.)		
<i>A. Wrightii</i> Gray (<i>A. vulgaris Wrightii</i> H. & C.)		
<i>A. biennis</i> Willd.		
<i>A. annua</i> L.		
<i>A. Bigelovii</i> Gray		
<i>A. Absinthium</i> L.	}	} <i>Absinthium</i> section
<i>A. frigida</i> Willd.		
<i>A. dracunculoides</i> Pursh. (<i>A. dracunculus glauca</i> H. & C.)		
<i>A. camptorum</i> Rydb. (<i>A. campestris pacifica</i> H. & C.)	} <i>A. campestris</i>	} <i>Dracunculus</i> section
<i>A. caudata</i> Michx. (<i>A. campestris caudata</i> H. & C.)		
<i>A. canadensis</i> Michx. (<i>A. campestris borealis</i> H. & C.)		
<i>A. pycnocephala</i> DC. (<i>A. campestris pycnocephala</i> H. & C.)		
<i>A. filifolia</i> Torr.		
<i>A. spinescens</i> D.C. Eat.		
<i>A. tridentata</i> Nutt.		<i>Seriphidium</i> section

Southernwood (*A. Abrotanum* L.), also called old man, and garden sagebrush, is a pleasantly scented shrub, resembling the coast sagebrush, 1½ to 5 feet high, with green and glabrous leaves with filiform divisions, much branched, erect or spreading and forming rounded bushes. The species is native of Europe but is much grown as an ornamental shrub in American gardens where it is hardy as far north as southern Canada. In Canada it is used as a windbreak and in Colorado as a nurse crop in reforestation. It is also frequently escaped in waste places. It flowers in August and October, and is regarded as a probable cause of hayfever in Minnesota and the eastern parts of the Dakotas where it is sometimes used as a hedge plant (ELLIS and ROSENDAHL 1932).

Coast sagebrush (*Artemisia californica* Less., *Crossostephium californicum* Rydb., fig. 71), also called California sagebrush, old man and various

other less appropriate names, is a rounded shrub with woody trunk, $2\frac{1}{2}$ to 4 feet high, and grayish leaves finely divided into linear segments.

Coast sagebrush is confined in distribution to the coastal strip of California, Lower California and adjacent islands, and is often extremely abundant on exposed slopes of hills, from 10 to 2500 feet elevation. Throughout much of this range it is associated with California mugwort. Flowering throughout the latter part of summer, it is reported to be a serious cause of hayfever (ROWE 1928, SELFRIDGE 1920, HALL 1917) and appears to be increasingly so. Of it HALL and CLEMENTS (1923) say: "The foliage is not regularly browsed by cattle, because of the strong odor and bitter taste, and, although browsed by sheep and goats, this is done only in the absence of more palatable food. As a result the hillsides of western California are in many places covered with a dense stand of this brush where more desirable species have been destroyed by sheep, goats and donkeys". It has been assigned to the genus *Crossostephium* by RYDBERG, but its pollen grains are typically those of *Artemisia*, lacking the vestigial spines which characterize the grains of the other species of *Crossostephium*.

The Vulgaris Group: — The following six species are so similar and closely related that HALL and CLEMENTS (1923) regard them as merely varieties or subspecies of the common mugwort (*Artemisia vulgaris* L.). They are herbaceous perennials, sometimes shrubby at the base, from a creeping rootstock, and with a peculiar pungent odor. Their stems are erect and mostly unbranched up to the inflorescence, striate or shallowly grooved and tinged with red in age. The leaves are enormously various in shape, but always white-tomentose beneath and frequently also above. The inflorescence is usually a broad panicle, the flower heads small with four to ten marginal flowers which are pistillate, and 3 to 50 disk flowers which bear both stamens and pistils.

The group is extremely various, some 80 different forms having been distinguished. Of these HALL and CLEMENTS (1923) recognize 15 distinct enough to merit subspecific rank. The following six are of special interest in hayfever studies. HALL and CLEMENTS state: "Preliminary studies indicate that the pollen of the different subspecies all react alike. Therefore, in testing and treating hayfever cases, the specialist need pay no attention to the complicated series of subspecies and minor variations". Many of these, however, have already found their way into the hayfever literature as separate species, so must be given attention here.

Common sagewort or mugwort (*Artemisia vulgaris* L., *Artemisia vulgaris typica* H. & C.) is a stout perennial herb, with erect stems 1 to $3\frac{1}{2}$ feet high arising from a creeping rootstock. The leaves are exceedingly various 1 to $4\frac{1}{2}$ inches long, deeply pinnatifid into linear oblong or somewhat spatulate pinnatifid toothed or entire lobes, densely white tomentose beneath and dark shining green above. The heads are small and numerous, erect, in panicles of simple or compound spikes.

Common mugwort is native of Europe and Asia. Introduced into America it is now found widely scattered from Newfoundland to Georgia

and westward to Alabama, Wisconsin and Manitoba. It flowers from July to October, shedding fairly large amounts of pollen but is seldom abundant enough to be of much importance in hayfever.

California mugwort (*Artemisia heterophylla* Nutt., *Artemisia vulgaris heterophylla* H. & C.) is very closely related and similar to the previous species, except that the leaves are less divided and broader, the principal leaves with a few prominent lanceolate lobes, varying to entire; like those of the foregoing species they are white-tomentose beneath and green above. But the flower heads are slightly larger.

California mugwort is common in the northeastern Rocky Mountain section from Saskatchewan to Idaho and on the Pacific coast from British Columbia to Lower California, and is the most abundant species in Oregon and California where it is the characteristic form of the bunch-grass prairies, but in California it has largely disappeared with the native grasses since it

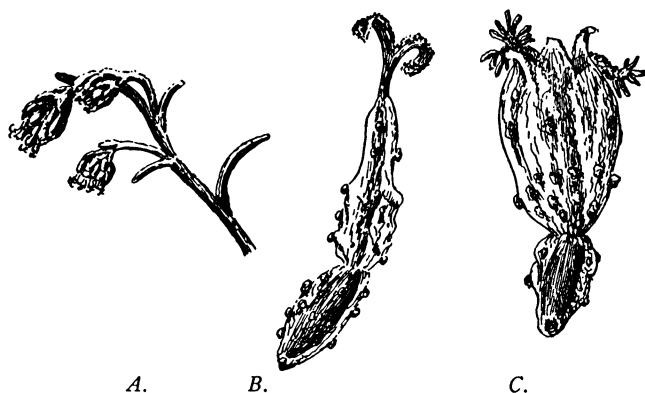


FIG. 71. — Coast sagebrush (*Artemisia californica*). A, Flowering spike; B, Marginal floret; C, Disk floret.

forms an important part of the late fall and winter feed for all classes of stock, especially sheep.

Dark-leaved mugwort, or prairie sage or wormwood (*Artemisia ludoviciana* Nutt., *Artemisia vulgaris ludoviciana* H. & C.), also called white sagebrush, is closely related and very similar to the two preceding species, except that the principal leaves are entire or variously toothed, rarely divided, and when so the lobes are short, their upper surface more thinly tomentose than the lower or at length becoming smooth and green. The inflorescence is an elongate narrow compact panicle, the heads more or less nodding, 12 to 20 flowered.

Prairie sage is abundant and widely distributed in western North America from Montana to Wisconsin, Kansas, Texas, Chihuahua, California, Washington and Idaho. It flowers from August to November and is known to cause much hayfever. The name, prairie sage, is less applicable

to this than to the next species, since it is "more typical of the foothill portions of the mixed prairie and runs high up in the great mountain parks, such as Estes Park", where on account of its shade tolerance it forms a ground cover in yellow pine woodland.

Prairie sage, western mugwort, or cudweed (*Artemisia gnaphalodes* Nutt., *Artemisia vulgaris gnaphalodes* H. & C.) is similar to the preceding species, so much so in fact that it is often included with it. It differs, however, in that its leaves are heavily tomentose on both sides, but this is almost the only constant distinguishing character. It is found in somewhat drier and less shaded positions, flowering at about the same time, and is the most characteristic sage of the true prairies. It is fairly abundant from Ontario and Michigan to Missouri, Texas, Coahuila, California, British Columbia and Saskatchewan.

Sawleaved mugwort or wormwood (*Artemisia serrata* Nutt., *Artemisia vulgaris serrata* H. & C., *A. ludoviciana serrata* H. & C.) is similar to the other members of the *vulgaris* group but distinguished by having lanceolate or linear-lanceolate pointed leaves with closely and rather evenly serrate margins. They are smooth and green above and white-tomentose below.

The sawleaved mugwort is restricted in distribution to the northern and central portions of the Mississippi valley where it is common and known to be an important cause of late-summer hayfever (ELLIS and ROSENDAHL 1933). It grows in good and rather moist soil, and is a larger plant than most of the members of this group, reaching a height of 10 feet. Though it is perhaps the most distinct of this group, it intergrades into both *A. ludoviciana* and *A. gnaphalodes*.

Gray sage (*Artemisia Wrightii* Gray, *A. vulgaris Wrightii* H. & C., *A. kansana* Britt.) is so closely related to *Artemisia ludoviciana* that it is impossible to draw a dividing line between them, but it may generally be distinguished by its smaller size for it scarcely reaches over two feet in height, and by the fact that its principal leaves are mostly divided into linear elongate or filiform lobes not more than 1 mm wide. All leaves are white-tomentose on both sides. It occurs from Kansas to western Texas and Chihuahua westward to Arizona and Utah and is particularly common in the arid portions of the southern Rocky Mountains. It is regarded as an important cause of hayfever in Utah (ANDERSON 1930).

Biennial wormwood or sagewort (*Artemisia biennis* Willd.) is an annual or biennial herb with a deep tap root and erect leafy stem, 1 to 3½ feet high, arising from a rosette of crowded leaves which are smooth and twice pinnately divided into lanceolate lobes. The stem is also smooth, but striate and often tinged with red, ending in a compound leafy spike of small flower heads. This species is closely related and similar to *A. annua*, distinguished chiefly by its slightly larger flower heads which are borne more or less erect in axillary spikes. It is widely distributed in North America, except in the southeast, but, according to HALL and CLEMENTS (1923), presumably native from the northern Rocky Mountain states to British Columbia. It is typically ruderal, growing occasionally in grass lands, but more generally

along roadsides and in waste places usually associated with other weeds. It is particularly abundant in the Mississippi valley from about the middle of Missouri northward. It flowers from August to December, producing large quantities of pollen which is the cause of much hayfever.

Annual wormwood or sagewort (*Artemisia annua* L.) is a tall annual with smooth stems and leaves, nearly inodorous, 1 to 3½ feet high, similar in habit and appearance to the preceding species to which it is closely related. But it may be distinguished by its smaller flower heads which are often nodding and borne in a wider and looser terminal panicle of lax racemes. It is native of Asia and eastern Europe but now naturalized throughout the eastern and central part of the United States as a weed in waste places and fallow fields. It flowers in summer but is nowhere abundant enough to be seriously regarded as a cause of hayfever.

Dwarf or flat sagebrush (*Artemisia Bigelovii* Gray) is a dwarf shrub with sprawling branches, closely resembling the low forms of *A. tridentata*. It has silvery-canescens leaves, oblong and three-toothed at the ends as in the common sagebrush, but their odor is faint and pleasant, but the two species are not regarded as closely related in spite of their outward similarity.

The dwarf sagebrush is common in the southern Rocky Mountains from southern Colorado and southern Utah to southwestern Texas and western Arizona. In the mixed prairie of northern New Mexico and Arizona it often forms a dominant society, also on rocky ridges especially in the cedar savannah, but it has a tendency to be replaced by the various grasses with which it is associated unless these are removed by grazing. It flowers in August and September, but is probably not more than a minor contributor to hayfever.

Common wormwood, sagewort or absinth sage (*Artemisia Absinthium* L.) is a tall spreading perennial herb with silvery, fragrant leaves, reaching a height of 6 feet. It is native of Europe but thoroughly established as a wayside plant throughout much of the northeastern United States and Canada and to a lesser extent westward. Flowering in August and September, it sheds only moderate amounts of pollen and the plants appear to be nowhere abundant enough at present to be more than a local and minor factor in hayfever, but they are spreading rapidly.

Pasture sage, prairie sage, carpet sage or estafiata (*Artemisia frigida* Willd.) is a low perennial herb generally woody at the base and with decumbent stems forming dense mats, with ascending annual stems seldom more than a foot high, with silvery leaves several times dissected into linear divisions. It is one of the most characteristic plant societies forming dense mats throughout most of the Great Plains and Rocky Mountain regions from Alaska to Texas. It flowers from July to October causing much hayfever, and appears to be increasing in importance. Of it HALL and CLEMENTS (1923) say: "Its abundance in the climax is partly the result of grazing, and is due to the position of the leaves in a mat. As a result it is one of the chief indicators of overgrazing on the Great Plains". Like *A. campestris* with which it is frequently associated, it is favored by disturbed soils.

Dragon sagewort or linear-leaved wormwood (*Artemisia dracunculoides* Pursh., *Artemisia Dracunculus glauca* H. & C.), also called Indian hair tonic and green sagebrush, smooth sagewort, tarragon, estragon, is a perennial herb with thick more or less woody rootstock, with erect stems, 2 to 4½ feet high. Its leaves and stems are nearly smooth and tinged with red, and not aromatic. It is found almost throughout the United States west of the Mississippi River where it is frequently common on the plains and mountain slopes. It flowers from July to November, and is regarded as a cause of hayfever in California (Rowe 1928). Of it HALL and CLEMENTS (1923) say: "The pollen . . . sometimes causes severe cases of hayfever in Western North America, its importance not so great as that of certain other species, such as *vulgaris* and *tridentata*, chiefly because it seldom occurs in quantity near cities".

The Campestris Group:— The following four species are so similar and closely related that HALL and CLEMENTS regard them as merely varieties of the field sagewort, *Artemisia campestris* L. They are biennial or perennial herbs, typically rosette formers, ½ to 2 feet high, scarcely odorous, their stems striate and nearly or quite smooth, ascending, often from a decumbent base, frequently tinged with red, their principal leaves variously divided into linear or almost filiform divisions rarely more than 1 mm wide, which are smooth or only slightly silky. The inflorescence is an elongate panicle with spike-like branches which are leafy below. The heads are small bearing from 5 to 20 marginal flowers which are pistillate, and 6 to 30 disk flowers which are staminate.

The members of the group are found on plains and in the mountains almost throughout North America, except in the desert regions. Though the various forms are often strikingly dissimilar in appearance, they are all alike in essential characters, and it is highly improbable that significant allergenic difference exist between them. Of the many different forms which have been segregated HALL and CLEMENTS recognize six which are worthy of subspecific designation. The following four are of particular interest to students of hayfever.

Field sagewort (*Artemisia camporum* Rydb., *Artemisia pacifica* Nutt., *A. campestris pacifica* H. & C.) is a perennial herb, 1½ to 2 feet high, erect from a spreading base, its principal leaves twice divided into narrowly linear divisions which are canescent or silky. It is the common form in the West, South Dakota and western Nebraska to New Mexico, Arizona, Oregon, Yukon and Saskatchewan. Flowering in late summer and fall it is an important cause of hayfever especially in the Rocky Mountain states. Of it HALL and CLEMENTS (1923) say: "It is one of the most unpalatable of artemisias to stock and hence is excelled only by *A. frigida* as an indicator of overgrazing. The pioneering quality of the species is also shown in [its] frequent occurrence . . . in disturbed soils, especially sands and gravels".

Tall wormwood (*Artemisia caudata* Michx., *Artemisia campestris caudata* H. & C., fig. 72) is a biennial herb usually with a single stem arising from a rosette of leaves which are twice or thrice pinnately cleft into filiform

or very narrow linear divisions. It flowers in August, shedding unusually large amounts of pollen which is undoubtedly a serious cause of hayfever where the plants are abundant. It is widely distributed principally on sandy shores and dunes or occasionally in waste places, most commonly in the eastern and central states. ELLIS and ROSENDAHL (1932) state that it is the commonest artemisia of the Upper Mississippi valley. It is fairly common throughout North and South Dakota and abundant in most parts of Minnesota except the northeastern corner, and is common around Minneapolis and St. Paul and on vacant lots within the cities.

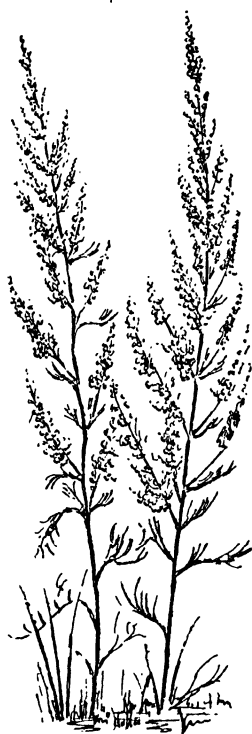


FIG. 72. — Tall wormwood (*Artemisia campestris caudata*).

Canadian mugwort (*Artemisia canadensis* Michx., *A. borealis* Pallas, *A. campestris borealis* H. & C.) is the northern form of the campestris group, ranging from Greenland and Hudson Bay to Vermont, western Ontario, Colorado and Washington. It flowers from July to August, but is of little consequence in hayfever.

Seashore mugwort (*Artemisia pycnocephala* DC., *A. campestris pycnocephala* H. & C.) is a small perennial herb not more than 2 feet high, with several or many erect stems arising from a small basal rosette of densely silky villous leaves. It is restricted to sandy beaches along the Pacific ocean from Oregon south to Point Sur, California. It flowers during summer and fall, but sheds relatively little pollen and is nowhere abundant. It is regarded as important in parts of California (Rowe 1928).

Silvery wormwood (*Artemisia filifolia* Torr.), also called sand sagebrush, is a rounded or straggling shrub reaching about 4 feet in height with mildly and pleasantly scented leaves which are ternately parted into filiform divisions or entire and filiform, often with smaller fascicled leaves in their axils. It is found often dominant in sandy soils from Nebraska and Wyoming to Nevada, Chihuahua and Texas and is perhaps the most widespread shrub on inland dunes and sand hills from Nebraska to Arizona. It is an important cause of hayfever during the latter part of summer.

Budbrush, budsage or spiny sagebrush (*Artemisia spinescens* D. C. Eat., *Picrothamnus desertorum* Nutt.) is a low spiny villous shrub scarcely reaching 1 foot in height, with leaves pedately divided and secondarily lobed with narrow divisions, with few flower heads which are solitary or arranged in small racemes in the axils or at the ends of short branches. Its achenes are ellipsoidal and densely arachnoid hairy. In its spinescent character and densely hairy flowers it differs from all other members of the genus, and this is regarded by RYDBERG and other authors as sufficient ground for separating the species from the artemisias and placing it in the monotypic genus *Picrothamnus* Nutt., but HALL and CLEMENTS regard these characters as relatively unimportant, developed in response to the unfavorable environment which it generally occupies. It is a shrubby dwarf rosette former of dry saline or alkaline soils. It is common on arid planes and slopes from Montana and Colorado to New Mexico, eastern California, eastern Oregon and Idaho. It flowers from March to June and is undoubtedly an important cause of hayfever.

Common sagebrush or mountain sagebrush (*Artemesia tridentata* Nutt.) sometimes erroneously called "black sage" is typically a shrub 3 to 12 feet high, but may be dwarfed by grazing or reach almost tree size under favorable conditions. It has a strong aromatic pungent odor. The main stem is usually trunk-like with dark shreddy fibrous bark, but the twigs are gray or white with a fine tomentum, ending in dense leafy panicles of numerous small heads of flowers which shed enormous quantities of pollen from July to late September.

The common sagebrush is the most abundant and important of all the artemisias as a cause of hayfever, in many places greatly outranking the ragweeds. HALL and CLEMENTS (1923) state that it is "the most common and widely distributed shrub of western North America especially on arid plains of the Great Basin, but ranging to timber line in the mountains; central Montana to North Dakota, eastern Colorado, New Mexico, Lower California, and eastern British Columbia". Throughout this wide area covering a variety of habitats, it occurs in a number of fairly well marked varieties some half dozen of which have received specific names. Fortunately, however, these have not yet found their way into hayfever literature. It is to be hoped that they will continue to be ignored for no possible advantage could be gained by their recognition. The species ranges in size from a dwarf similar in appearance to *A. Bigelovii*, usually the result of overgrazing, to a small tree 20 feet high. It forms the bulk of the vegetation of the Great Basin and ranges into the mixed prairie and bunch-grass prairie, especially where overgrazing has given it an advantage in competition with the grasses. This is especially true in eastern Oregon, north-eastern California, and southern Idaho where the original grass land has been almost completely replaced by sagebrush. It is eaten by grazing animals only when nothing else is available, but because it can be used to carry stock through the winter it is not regarded with disfavor. So if

current grazing practices are allowed to continue, sagebrush promises to become an even more serious cause of hayfever than it already is.

Senecioneae: — The groundsel tribe is a large group, next to the *Astereae* the largest in the family, comprising more than 1400 species, but about 1200 of these belong to the genus of groundsels (*Senecio*), the largest genus of the family. Apparently all are insect pollinated and of no consequence in hayfever.

Cynareae: — The thistle tribe includes such familiar forms as the thistles (*Cirsium*, *Carduus*, *Cnicus*), the burdocks (*Arctium*), the globe thistles (*Echinops*), the star thistles (*Centaurea*) and the globe artichoke (*Cynara Scolymus* L.). They are distinguished by having only perfect and tubular flowers with corollas deeply five-cleft. They are insect pollinated and exceptionally well adapted to this mode of pollination so that it is unlikely that their pollen could ordinarily cause hayfever, though some of the thistles, especially the bull thistle (*Cirsium lanceolatum* Hill) and the Canada thistle (*C. arvense* Scop.) have been suspected of doing so.

The pollen-grain forms of this tribe are exceedingly various in all their characters. They are mostly large, generally over 40μ in diameter, in the globe thistle (*Echinops sphaerocephalus* L.) reaching 70μ in length. Generally the exine is very thick and coarsely granular. The furrows are extremely various but are usually short or of medium length, occasionally so short as to coincide in extent with the enclosed germ pore (*e.g.*, some species of star thistle). Occasionally the furrows are long and tapering as in the grains of burdock (*Arctium Lappa* L.). The spines when present tend to be broadly conical, but in the grains of many species they are represented by the merest vestiges (the globe thistle, some species of star thistle and blessed thistle *Cnicus benedictus* L.), or entirely absent (some species of star thistle).

Mutisieae: — The mutisia tribe is almost entirely South American and South African, though represented in the West Indies by a few shrubby and herbaceous forms, and in the southern part of the United States by such forms as *Trixis* and *Perezia* of California, and *Chaptalia* of Florida and the Gulf states. The group is, however, best known in America through the Natal or African daisy (*Gerbera Jamesoni* Bolus) which, though native of South Africa, is extensively cultivated and a well known hot-house plant with beautiful daisy-like flower heads with long narrow and variously colored rays rising on naked stalks from a rosette of broad basal leaves. The flower heads of the others are either with or without rays, the corollas commonly five toothed and bilabiate or, less frequently merely deeply five cleft, suggesting a close relationship with the thistle tribe.

The pollen grains of the mutisia tribe represent several distinct and apparently unrelated forms. This, it appears, is probably because the tribe is not a natural group. The grains of most resemble those of the thistle tribe, having thick, coarsely granular exine, furrows of medium length, and spines, when present, broad and short but the spines are generally repre-

sented only by vestiges, reminiscent of the grains of most of the star thistles and in one small subtribe, the *Nassauvinae*, and the South American genus *Barnadesia* they are entirely absent. The grains of the latter are quite different from those of all other members of the tribe. They are characterized by elaborate sculpturing resembling that of the grains of the *Cichorieae* except for their lack of spines. There is, however, evidence to show that both the *Nassauvinae* and *Barnadesia* are not genetically closely related to the rest of the tribe nor to each other. This interesting phase of the subject has been discussed in greater detail elsewhere (WODEHOUSE 1928c, 1929a, 1929b, 1935).

Cichorieae: — The chicory tribe comprises about 70 genera and 1500 species, mostly herbs with milky juice. They differ from all other members of the family in having all flowers of the heads perfect and with strap-shaped corollas generally five-toothed at the apex. This is the most distinct and sharply separated tribe of the family and, as has already been pointed out, is regarded by some botanists as a separate family (*Cichoriaceae* Britton and Brown) or as a subfamily or series, *Liguliflorae* Gray. Nevertheless there is no doubt that the group belongs to the Composite family and it is generally believed to be rather closely related to the two preceding tribes.

The *Cichorieae* are well known to us through such familiar and useful species as the common chicory (*Cichorium Intybus* L.), endive (*C. Endivia* L.), lettuce (*Lactuca sativa* L.), oyster plant or salsify (*Tragopogon porrifolius* L.), black salsify (*Scorzonera hispanica* L.), and the Spanish oyster plant (*Scolymus hispanicus* L.). All are strictly insect pollinated, and though several species are common and troublesome weeds, only one, the common dandelion (*Taraxacum officinale* Weber), has ever been suspected of causing hayfever. The dandelion is said to be an important contributor to early summer hayfever in the Pacific Northwest (STIER, HOLLISTER and BONSER 1930) and in Utah (ANDERSON 1930, BARRETT 1934).

The pollen grains (fig. 58B) of the *Cichorieae* are widely divergent from the basic form of the family. They have the three characteristic furrows and pores, but with few exceptions are distinctive in having an elaborate and beautiful system of sculpturing. Their exine is thrown into high vertical spine-topped ridges which divide the surface of the grain into angular lacunae. The number and arrangement of these is various in the different species but they are nearly always arranged in symmetrical patterns of striking beauty. In this respect they resemble the grains of the ironweed tribe but may be distinguished by their simple patterns, composed of 6 to 21 lacunae as compared with 30 or more in the grains of the ironweeds. These beautiful grains have been made the subject of an extensive study by the author and reported elsewhere (WODEHOUSE 1935).

Chapter IV

REGIONAL SURVEYS

In recent years as the necessity for a knowledge of the local hayfever flora is becoming more generally understood among students of hayfever more and more regional surveys are being reported. A search of the medical literature to date has brought to light about 135 reports of regional surveys which seemed worthy of consideration. All but a few states are represented by at least one report, some by many. As would be expected these are not at all evenly distributed over the country, but tend rather to follow the concentrations of population, coming in greatest frequency from the states on or near the Atlantic seaboard, and next from those of the Pacific, with the central part of the country, except for the Great Lakes region, and Colorado and Utah, very poorly represented. The reports vary in comprehensiveness from a casual observation of a plant or two, to careful and painstaking studies often conducted over several years, and in scope from those covering a single community or town to those covering whole states or groups of states.

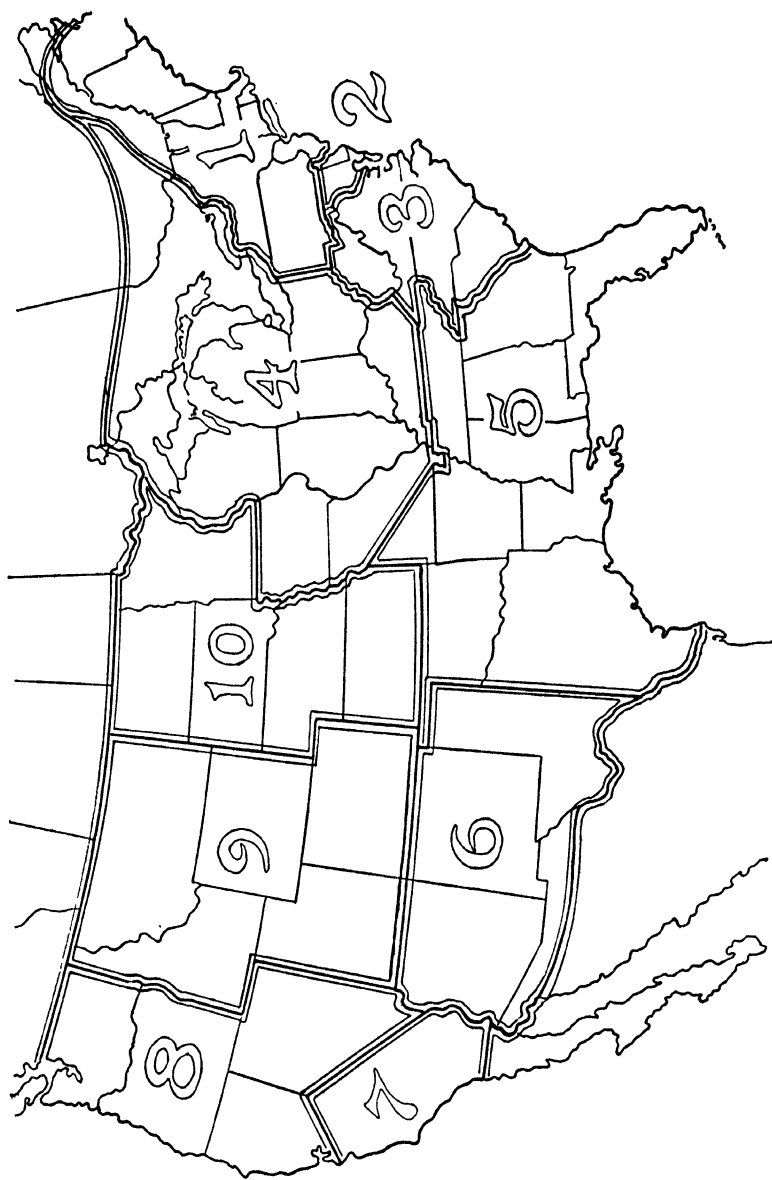
The present chapter is largely a compilation of these reports. For convenience of presentation the country is divided into ten sections as indicated on the accompanying map. These divisions are arbitrarily chosen; their size and arrangement is entirely a matter of convenience in presenting the data.

Most of the published reports of surveys include many species which are of little consequence in hayfever, or none whatever. As far as possible I have tried to eliminate these, and still include in the tables all those which appear to be important enough to merit consideration in the diagnosis and treatment of hayfever occurring in the region represented. Those which are of primary importance are printed in bold face type.

The flowering periods recorded in the tables are for the most part composites of a number of reports, generally varying somewhat. Each week of the flowering span of a species is represented by a vertical stroke, the dark strokes representing general flowering, the light strokes representing local or less general flowering.

I. The Northeastern States (New England States, New York, New Jersey and Pennsylvania):—

Hayfever in this region falls into three well marked seasons: the early-spring or tree season which starts with the first appearance of spring, generally early in April, and extends well into May; the late spring or early-summer season, which is also called the grass or grass-plantain season, starting about the middle of May and lasting until the middle of July; and the late-summer or ragweed season which starts very definitely at about the middle of August, in some places always exactly on the 15th, and generally fades out toward the end of September, not on account of



THE TEN HAYFEVER REGIONS OF THE UNITED STATES.

frost as generally stated, but with the normal going-to-seed of the late-summer vegetation.

Early Spring Hayfever:— Of these three seasons the first, or tree hayfever season, is the least important in spite of the fact that during this time the pollen in the air reaches its maximum concentration; the pollen of oak alone occurs in much greater abundance than that of ragweed in the later season, and the pollen of the birches is almost its equal, yet relatively few cases of hayfever from these or other tree sources are recorded. But those which do occur may be very severe, and generally several species are involved (TUFT and BLUMSTEIN 1937).

Table I, HAYFEVER PLANTS OF THE NORTHEASTERN STATES: —
(New England States, New York, New Jersey and Pennsylvania)

SPECIES	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
<i>Ulmus</i> * (Elms)				III								
<i>Acer</i> * (Maples)				III	III							
<i>Salix</i> * (Willows)					III							
<i>Populus</i> * (Poplars)				II								
<i>Betula</i> * (Birches)					III							
<i>Quercus</i> * (Oaks)					III							
<i>Fagus</i> (Beeches)					III							
<i>Fraxinus americana</i> (White ash)					III							
<i>Alopecurus pratensis</i> * (Meadow foxtail)						II						
<i>Anthoxanth. odorat.</i> (Sw. vernalgrass)						II						
<i>Plantago lanceolata</i> * (English plantain)						II		III	III			
<i>Poa pratensis</i> (June grass)						II	III	III				
<i>Dactylis glomerata</i> (Orchard grass)						II	III	III				
<i>Rumex Acetosella</i> (Sorrel dock)						II	III	III				
<i>Festuca rubra</i> (Red fescue)						II	III	III				
<i>Festuca elatior</i> (Meadow fescue)						II	III	III				
<i>Poa compressa</i> (Canada bluegrass)						II	III	III				
<i>Phleum pratense</i> (Timothy)						II	III	III				
<i>Agrostis alba</i> (Redtop)						II	III	III				
<i>Iva oraria</i> * (Marshelder)							III	III	III			
<i>Solidago</i> * (Goldenrods)							III	III	III			
<i>Ambrosia elatior</i> (Short ragweed)							III	III	III			
<i>Ambrosia trifida</i> (Tall ragweed)							III	III	III			
<i>Xanthium</i> (Cocklebur)							III	III	III			

* Discussed in the paragraphs immediately following.

Elms.— The commonest elm is the white (*Ulmus americana*), prevalent throughout the region. Also fairly common is the slippery elm (*U. fulva*) and in the New England States, particularly in the region of Boston, is the European elm (*U. campestris*), formerly commonly planted along city streets and in parks.

Willows.— Many species of willow occur in the region. The commonest are the European purple osier, pussy willow (*Salix discolor*), black, crack and weeping willows.

Maples.— The commonest are silver, red, sugar, Norway and sycamore maples, and box elder. The latter sheds much more pollen than the others but is rather localized in distribution, and seldom common.

Poplars. — Many species of poplar occur. The commonest are the European white and black poplars, large-toothed and trembling aspens, the necklace poplar, tacamahac and Carolina poplars. They all flower at about the same time.

Birches. — The three commonest species of birch are the gray (*Betula populifolia*), yellow and black, flowering in succession and with their periods overlapping. The paper birch occurs naturally in the northern part of New England and Pennsylvania, and it and the European white birch are frequently planted in city parks and streets. The birches rank perhaps second to the oaks in importance, and the cases of hayfever from their pollen which have been recorded appear to be very severe.

Oaks. — Many species of oak occur in this region; the commonest are black (*Quercus velutina*), Spanish, white, chestnut, swamp-white and shrub oak (*Q. ilicifolia*). They all flower at about the same time and it is to their combined efforts that is due the enormous pollen count that is recorded during about the two weeks in the middle of May. Oak is probably the most important tree pollen in the region. Nevertheless not very many cases are recorded even from it, but those which do occur are often severe.

Often included in pollen lists for this region are sweet gum and eastern sycamore, but neither of them appears to be of importance in hayfever.

Early Summer Hayfever: — The second or grass-plantain season is very much more important than the first season. It starts early in May when sweet vernalgrass begins to flower. This is quickly followed by June grass, orchard grass, timothy and redbud, flowering more or less in succession. These five species appear to be responsible for nearly all the grass hayfever. There are, however, a number of other grasses which are of some importance locally. For example, red fescue, meadow fescue and wild oatgrass (*Danthonia spicata*) are heavy pollen shedders but seldom abundant enough to be very important. Quack grass (*Agropyron repens*) is only a meagre pollen shedder. Meadow foxtail (*Alopecurus pratensis*) is locally abundant particularly in the New England States. It is a heavy pollen shedder similar to timothy and may occasionally be a local factor of importance. Canada bluegrass is said to be important in parts of Pennsylvania (SCOTT, CRIEP and GREEN 1936) and eastern Massachusetts (RACKEMANN and SMITH 1931b), but though it occurs elsewhere it is not common enough to be of much importance.

There are several species of plantain distributed abundantly throughout the region, but of these only the English plantain is a factor in hayfever.

Late Summer Hayfever: — The third, the ragweed, season is by far the most important, accounting for many more cases of hayfever than the other two together. The hayfever of this season is due practically entirely to the pollen of the short and tall ragweeds. In the New England States and Maritime Provinces it is almost entirely the short ragweed, the tall ragweed being either entirely absent or occurring only sparingly. In the southern and western part of the region, however, the tall ragweed is fully as abundant as the short, and often much more so.

Several species of cocklebur are found scattered along railroad embankments, roadsides, river courses, etc., but they are never very abundant and the records of the pollen slides show that their pollen is not an important factor. There are many species of goldenrod growing profusely throughout the area but most of them shed too little pollen to merit consideration, and not until the showy goldenrod (*Solidago speciosa*) comes into flower in September does goldenrod pollen appear on the slides, then for a short period it may even outrank cocklebur pollen.

Marshelder (*Iva oraria*) grows in great abundance in the tidal marshes along the coast and appears to be occasionally a local cause of hayfever.

Pigweed, Mexican tea and lambsquarters grow abundantly throughout the region and their pollen may be detected in small amounts in the air during most of the summer, but there is no evidence to suggest that they are of any importance in hayfever.

Marsh grass (*Spartina patens*) is extremely common in tidal marshes all along the coast and may be a local contributor to midsummer hayfever. RACKEMANN and SMITH (1931*b*) include it in their list of hayfever plants of eastern Massachusetts, and it appears to be a contributor to late-summer hayfever on parts of Long Island.

REFERENCES

The earliest report is that of WALKER (1921). He reports 12 cases sensitive to pollen of trees, including one each to that of oak, maple and willow, all of which were benefited by treatment with extracts of the corresponding pollen; and one each to the pollen of pine, poplar and ash, which were not treated. VANDER VEER, COOKE and SPAIN (1927) with the help of Professor HODGSON of Montclair, N. J., made an exhaustive study, presumably applicable to the entire area of the northeastern states, and constructed a useful pollen calendar, showing the flowering periods of 50 or more plants common in this area which present hayfever possibilities. This report also gives the different kinds of pollen which were used in treating a random group of hayfever cases. Ragweed tops the list with 696 cases, timothy second with 420 and plantain third with 237, but birch, oak and goldenrod were used in only 59, 56 and 14 cases respectively.

RACKEMANN and SMITH (1931*a*, 1931*b*) give a useful list of hayfever plants of New England with their dates of flowering, and state that meadow fescue, meadow foxtail, lambsquarters, artemisias, cocklebur and tall ragweed, while occurring in New England, are not found in stands large enough to be significant. WILMER and COBE (1932) exposed oiled slides in Philadelphia, Pa., and showed that the fluctuations in the pollen count corresponded to symptoms of hayfever.

The present author (WODEHOUSE 1933) reported in the form of a graph a record of all the different kinds of pollen caught on atmospheric pollen slides coated with glycerine jelly throughout one entire hayfever season in Yonkers, N. Y. More than 35 different kinds were identified and their dates of appearance and relative abundance recorded. These showed that the pollen of the oaks greatly outranked that of the ragweeds and that of birch approximately equalled it, and that during the month of May the combined count of all atmospheric pollen is very much higher than at any other time.

FREUD (1935) published a list of anemophilous plants with hayfever possibilities of the Capitol District, New York. SCOTT, CRIEF and GREEN (1936) reported atmospheric pollen counts of the grasses, chenopods and ragweeds for the region of Pittsburgh, Pa., including Canada bluegrass among those of first importance. THOMMEN (1930) discussed the importance of spring hayfever in the northeastern states, including a table of the pollination periods of the most important trees causing hayfever in the section east of the Mississippi River and north of Tennessee and North Carolina.

PRATT (1938) and PRATT, COLMES, FROMER, GREENE, CHAFEE and CLAPP (1941) report mold and pollen surveys of southeastern New England. Grass and weed pollen they find to be more abundant in the suburbs than in the cities, and *Alternaria* spores are most abundant during the ragweed season.

Several of the standard textbooks devote a few pages to the botanical aspects of this region; VAUGHAN (1931) gives a list of "The more common plants of New England producing light dry pollen" compiled by Professor M. L. FERNALD of Harvard University, and reported by RACKEMANN (1931). THOMMEN (1931) lists with their flowering periods, the trees, grasses and weeds which are believed to be the most important causes of hayfever in the vicinity of New York City. HANSEL (1936) gives a brief summary of the literature dealing with the New England States and New York. RACKEMANN (1931) gives a brief summary of some of the regional surveys, including FERNALD's original list of plants with hayfever possibilities and their times of flowering in the New England States.

Hayfever Resorts:— Few places in this region are entirely free from ragweed pollen. In New York State much of the Adirondack Mountain region is nearly free from ragweed pollen, particularly Hamilton and Franklin counties, owing to the fact that these regions are still heavily wooded. The New York State Department of Health (Anonymous 1943) has fully recognized the value of these places as hayfever resorts and is taking determined steps to keep them free. From the Department may be obtained without charge detailed information and maps of the free areas.

Great South Beach on Long Island is variously reported. It is a long sandy strip lying off the south shore of the Island with Great South Bay between. There is only an insignificant amount of ragweed growing on the Beach so that the patient's chances of freedom from hayfever depend upon the unpredictable direction of the wind. A land breeze brings little or no relief but a sea breeze brings nearly complete freedom from pollen. The region of Montauk Point at the extreme eastern end of Long Island is somewhat better situated and can be counted on as nearly free from ragweed pollen.

Large sections of Maine which still remain heavily forested are comparatively free from ragweed pollen. SYLVESTER and DURHAM (1938) and SYLVESTER (1939a) report a study of the hayfever situation in Maine. Throughout most of the state the hayfever season is short and the load of atmospheric pollen light; Portland has 18 days of hayfever but the northern section of the state (Aroostook County) is nearly free. Elsewhere in the state the region of Rangeley Lake, Machias and Greenville experience not more than three days each season of pollen sufficiently heavy to cause hayfever.

The White Mountains in New Hampshire have long been famed for their freedom from hayfever. The principal resort is Bethlehem. It owes its advantage to its elevation and short growing season which prevent the growth of ragweed plants, and to the fact that much of the surrounding territory from which pollen might be blown, is still heavily forested.

Much of Nova Scotia is free from ragweed pollen, particularly the parts which still remain heavily timbered. But the famed Annapolis Valley has an abundance of ragweed from which many cases of hayfever are recorded.

II. The Middle Atlantic States (Delaware, Maryland and District of Columbia):—

Early Spring:— Hayfever of this region falls into the same seasons as in the New England States. The early spring or tree hayfever season accounts for about 4.4 per cent of the cases (BERNTON 1923). It starts early in March with the maples and elms, followed by several species of poplar and ash, but these are all of relatively little importance. The oaks which flower a little later are by far the most important of the trees. According to BROWN (1932), "There are at least 20 different species growing in the Middle Atlantic States", the principal species being the black (*Quer-*

cus velutina), white and red oaks. All species flower at about the same time and account for about 45 per cent of the tree cases (BERNTON 1930). Next in importance among the trees are the eastern sycamore and hickories, each accounting for about 13.7 per cent of the tree cases. Four species of hickory, *Carya cordiformis*, *C. alba*, *C. ovata* and *C. glabra*, are common in the region, but they are not generally distinguished from each other in hayfever studies. Of peculiar interest in this region is the paper mulberry (*Broussonetia papyrifera*). Though it accounts for relatively few cases

Table II, HAYFEVER PLANTS OF THE MIDDLE ATLANTIC STATES: —
(Delaware, Maryland and District of Columbia)

SPECIES	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Acer (Maples)												
Acer Negundo (Boxelder)												
Acer platanoides (Norway maple).....												
Ulmus (Elms)												
Populus deltoides (Necklace poplar)....												
Fraxinus americana (White ash).....												
Betula alba (White birch)												
Betula nigra (Red birch)												
Salix (Willows)												
Quercus* (Oaks)												
Carya (Hickories)												
Fagus grandifolia (American beech)....												
Platanus occidentalis (Sycamore)												
Juglans nigra (Black walnut)												
Juglans cinerea (Butternut)												
Broussonet. papyrif. (Paper mulberry)												
Anthoxanth. odorat. (Sw. vernalgrass)												
Plantago lanceolata* (English plantain)												
Rumex Acetosella (Sorrel dock).....												
Dactylis glomerata (Orchard grass)...												
Poa pratensis (June grass)												
Festuca elatior (Meadow fescue)												
Lolium perenne (Perennial ryegrass)...												
Agrostis alba (Redtop)												
Phleum pratense (Timothy)												
Cynodon Dactylon* (Bermuda grass)....												
Iva frutescens (Marshelder)												
Ambrosia trifida (Tall ragweed)												
Ambrosia elatior (Short ragweed)												
Xanthium (Cocklebur)												

* Discussed in the accompanying paragraphs.

(5.8 per cent of the tree cases) these may be very severe and are likewise sensitive to pollen of the related mulberries and Osage orange (*Maclura pomifera*) which also grow in this region (BERNTON 1928). Next in importance are the birches; several species occur but the principal one is the red or river birch. The poplars are relatively unimportant; though the trees are abundant they are principally Carolina poplar which sheds but little pollen.

Late Spring:— Among the causes of hayfever during the late spring or early summer season, orchard grass is the most important (AQUARONE

and GAY 1931), greatly outranking timothy. Indeed the latter is found to be of little importance in Baltimore. Other grasses which contribute to the hayfever of this season are much the same as those recorded for the New England States, except that Dallis grass, Bermuda grass and other southern species are reported to occur in this region, but they appear to be of little consequence.

Plantain. — BERTON (1925) finds that in this region plantain pollen accounted for 4.3 per cent of a series of hayfever cases, and AQUARONE and GAY (1931) have designated this period the plantain season, since its flowering period bridges the gap between the early and late summer hayfever seasons, extending from July 1 to August 15.

Late Summer: — Hayfever in the late-summer season appears to be due almost entirely to the pollen of the short and tall ragweeds, contributed to slightly by cocklebur, and locally by marshelder.

REFERENCES

The earliest record is that of BERTON (1923) in which is published a list with dates of flowering of all plants with hayfever possibilities of the Baltimore region. The same author discovered the importance of plantain (BERTON 1925) and paper mulberry (BERTON 1928).

Similar work was done by BROWN (1927) for the District of Columbia, dealing only with the late-spring or early-summer season. He showed that 12 out of 13 of the cases suffering from hayfever at this time were sensitive to the pollen of sweet vernalgrass, June grass, orchard grass, timothy and redtop, and about one sixth were sensitive to the pollen of plantain. In a later paper BROWN (1932) extended his observations to include the whole of the Middle Atlantic States and all seasons. He states that the early-spring season accounts for 4 per cent, early-summer 32 per cent, and late-summer 64 per cent of the hayfever cases. Among the trees he states that the oaks are the most important, sycamore next, and "The hickories of which there are at least seven different species in the Middle Atlantic States are responsible for quite a few cases".

AQUARONE and GAY (1931) made a pollen survey of Baltimore exposing at the same time oiled pollen slides. Their report presents a list of plants which cause hayfever, and others of which the pollen becomes atmospheric, together with their dates of flowering. Pollen counts are reported as graphs showing the record of grass, plantain and ragweed. The peak of the grass curve, about 400 grains per square centimeter of slide surface, occurred about the first of June and is accounted for by orchard grass. "*Plantago lanceolata* pollen appeared at a surprisingly constant rate of about 25 grains per square centimeter daily from mid-May to early August." The ragweed curve showed two major peaks, August 28 and September 19, reaching about 160 and 180 grains per square centimeter respectively. This work was extended by PATTERSON and GAY (1932), giving a useful schematic chart of the pollination periods of the different trees, grasses and weeds of Baltimore, and curves for pollen counts of pine, oak-beech, plantain, grass, mold spores and ragweed. Oak-beech pollen reached its peak of 351 grains per square centimeter on May 5, pine 104 on May 2, hickory 47 on May 1. Plantain reached a peak of only 21 grains on June 15 while grass pollen scarcely reached 15.

Several of the standard textbooks devote a few pages to the hayfever of this region. HANSEL (1936) and VAUGHAN (1939) give brief reviews of the literature summarizing the results of all the important contributions to our knowledge of the hayfever of this region. VAUGHAN (1931) reprints the more important tables from BERTON's publications.

III. The Virginias and Carolinas (Virginia, West Virginia and North and South Carolina):—

The Maples.—Several species of maple are represented and appear to be rather important. Silver, red, sugar and Norway maples are common

Table III, HAYFEVER PLANTS OF THE VIRGINIAS AND CAROLINAS:—
(Virginia, West Virginia and North and South Carolina)

SPECIES	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Acer* (Maples)												
Acer saccharum (Sugar maple).....												
Acer Negundo (Boxelder)												
Ulmus* (Elms)												
Juniperus virginiana* (Red cedar).....												
Salix (Willows)					—							
Corylus (Hazel)												
Betula lutea (Yellow birch)			—									
Betula lenta (Black birch)			—									
Betula nigra (Red birch)												
Quercus* (Oaks)												
Taxodium distichum (Cypress)			—									
Juglans cinerea (Butternut)												
Juglans nigra (Black walnut)												
Populus (Poplars, cottonwood)												
Platanus occidentalis (Sycamore)												
Fagus grandifolia (American beech)....												
Morus (Mulberries)												
Celtis occidentalis (Hackberry)												
Fraxinus americana (White ash)												
Fraxinus pubescens (Red ash)												
Liquidambar Styraciflua (Sweet gum)..												
Carya Pecan (Pecan)												
Carya* (Hickories)												
Broussonet. papyrif. (Paper mulberry)..												
Poa annua (Annual bluegrass).....												
Lolium perenne (Perennial ryegrass)....												
Rumex Acetosella (Sorrel dock)												
Plantago lanceolata (English plantain)												
Anthoxanth. odorat. (Sw. vernalgrass).												
Dactylis glomerata (Orchard grass)....												
Holcus lanatus (Velvet grass).....												
Poa pratensis (June grass)												
Poa trivialis (Rough meadowgrass)												
Chenopodium album (Lambsquarters) ..												
Amaranthus spinosus (Spiny amaranth)												
Amaranthus retroflexus (Pigweed).....												
Festuca rubra (Red fescue).....												
Festuca elatior (Meadow fescue).....												
Phleum pratense (Timothy)												
Agrostis alba (Redtop)												
Cynodon Dactylon* (Bermuda grass)												
Sorghum halepense (Johnson grass)												
Paspalum dilitatum (Dallas grass).....												
Iva frutescens (Marshelder)												
Cyclachaena xanthifolia (Burweed)												
Ambrosia bidentata (Southern ragweed)												
Ambrosia trifida (Tall ragweed)												
Ambrosia elatior (Short ragweed)												
Xanthium (Cocklebur)												

* Discussed in the accompanying paragraphs.

and flower very early, but perhaps even more important is the boxelder (*Acer Negundo*) since it is entirely wind pollinated and rather common.

The different species flower more or less in succession and show a wide range in their flowering periods depending on weather conditions, hence the long flowering period shown in the table. VAUGHAN, GRAHAM and CROCKETT (1933) record silver maple and red maple flowering in January.

Elms. — Three species of elm are common to the region, the winged, white and cork elms, the former which is frequently planted as a street tree, preceding in its flowering the two latter by several weeks. It is recorded as early as January (VAUGHAN, GRAHAM and CROCKETT 1933).

Junipers. — Both the red cedar (*Juniperus virginiana*) and the common juniper (*J. communis*) are common in the region. They usually flower in April but are recorded as early as February.

Hickories. — The hickories, including pecan, appear to rank rather high as causes of hayfever but the various species are not usually distinguished in hayfever studies. *Carya cordiformis*, *C. minima*, *C. ovata*, *C. alba*, *C. glabra* and *C. Pecan* are recorded for the region. They all flower at about the same time, during the last weeks in April and the first in May.

Oaks. — There are many different species, including such as *Quercus rubra*, *Q. palustris*, *Q. nigra*, *Q. Phellos*, *Q. alba*, *Q. virginiana*, *Q. coccinea* and others. On account of the wide variation of their flowering periods influenced by weather conditions, oak pollen may be found in the air throughout April and May and sometimes even longer.

Poplars. — The European white poplar (*Populus alba*) is reported (BLOMQUIST and OOSTING 1936) to be fairly common in North Carolina, spreading by root suckers and forming thickets about old home sites. The necklace poplar (*P. balsamifera virginiana* Sarg.) is fairly common in moist soil along streams and lakes, also some of the cultivated varieties and hybrids.

Bermuda grass is important principally in the southern part of the region and is abundant in Charleston.

Several species of mugwort, as *Artemisia annua*, *A. biennis* and *A. frigida* are reported to grow in the region but are scarcely abundant enough to be important. Russian thistle is also occasionally observed but is not regarded as a cause of hayfever. Sorrel dock (*Rumex Acetosella*) is abundant and sheds a good deal of pollen which may occasionally be a factor to be reckoned with.

REFERENCES

The hayfever problem in Virginia has been thoroughly studied by VAUGHAN and his co-workers and the results of their work is admirably reported in their six years' survey (VAUGHAN, GRAHAM and CROCKETT 1933) in which they give a list, with their flowering periods, of all the plants with hayfever possibilities. They emphasize the fact that there is much variation from season to season and in different localities, particularly among the trees and to a lesser extent among the grasses. They point out, for example, that June grass may be flowering in Richmond as early as January 15, though it ordinarily does not flower until June. VAUGHAN (1931) gives a complete list of 'Airborne Pollen Plants of Southern and Western Virginia' prepared by HORATIO S. STAHL, and a list of 'Hayfever Plants in the Vicinity of Richmond, Va.' prepared by ANNA CLARK. The first two of these lists state the time of flowering of the various species, while the latter states their relative abundance. VAUGHAN in another list in the same publication gives the relative frequency of positive sensitizations found to the

various hayfever species as compared with ragweed in Virginia and the Carolinas. Giving short ragweed a rating of 100, the grasses are found to range from 2 to 28, hickory 14, plantain 22.

BLANTON (1932) gives a list of the 'Pollination periods of trees east of Mississippi and north of North Carolina', and records of the pollen counts on oiled slides for the total amount of pollen. The chief trees in Richmond, he states, are pin oak, maples, elms, cottonwoods, ginkgo, mulberries, sycamore, poplars and catalpa. He also states that none of his hayfever cases reacted to plantain pollen.

HOCH and WARING (1933) published a classified list of plants with hayfever possibilities for Charleston, S. C. and vicinity within a radius of 10 miles, and furnish a key which 'may be used as a helpful guide in determining the prevalence . . . of the more important pollens of this section.'

TODD (1934) reports his observations on the local flora and the results of daily atmospheric pollen counts in Charlotte, N. C. as recorded on oiled slides, both by the 24 hour gravity count and the 5 minute blower count devised by DUKE. He reports maple and elm flowering January 31, but the grasses, he says, begin to show on the slides in definite numbers on April 7, rapidly increasing throughout the month, and he emphasizes the importance of the trees and grasses in this section, especially the grasses because their pollen carries on, showing even increased counts during the main part of the ragweed season, making it necessary to combine grass and ragweed pollen in treating patients for the late-summer hayfever. His figures also show that in 1933 Charlotte's total pollen count of 1,563 is $2\frac{1}{2}$ times as high as Charleston's and $\frac{2}{3}$ that of Raleigh as reported by O. C. DURHAM, and that Charlotte's daily average ragweed count is higher than that of Richmond, Philadelphia and New York.

COCKE (1938*b*) reports an atmospheric survey of Charlottesville, Virginia for the year 1936. He gives a list of the wind pollinated trees, grasses and weeds and the record of 46 different kinds of pollen caught on his atmospheric pollen slides. This should prove one of the most useful reports for students of hayfever in Albermarle County.

These studies show that hayfever in the Virginias and Carolinas, as compared with that of more northern sections, is of longer duration, starting earlier and ending later, more various from year to year and from place to place, and is practically continuous throughout the growing season, not occurring in three well marked seasons as in the more northern provinces. Also a large number of species of plants are involved, and the trees and grasses assume relatively greater importance. Albeit hayfever here is no worse and, as in most places in the East, is mainly caused by the tall and short ragweeds.

IV. The North-Central States (Ohio, Kentucky, Indiana, Michigan, Illinois, Iowa, Eastern Missouri, Wisconsin and Southern Ontario):—

The flora of the north-central region is in the main, eastern in character, and in its principal elements is similar to that of the northeastern states. The same three hayfever seasons may be recognized, that of the early spring due to the pollen of trees, that of the late spring or early summer, due principally to the grasses, and that of the late summer due principally to the ragweeds. Of these the earliest season is of relatively little importance, even somewhat less than in the Northeast. The second season is much more important, but the greater part of the hayfever occurs in the late summer season. As in the Northeast, June grass, orchard grass, timothy and redbud account for the major portion of early-summer hayfever, and the ragweeds, especially the short, are much the most important of all, accounting for approximately 90 per cent of the late-summer hayfever.

But the north-central flora also contains elements encroaching on it from the West and the South. Thus Russian thistle flourishes in some sections including parts of the

Chicago area and Indiana, and prairie ragweed or burweed marshelder, also a western species, occurs abundantly in and about Chicago where it is one of the most important local causes of hayfever. Western ragweed, a far-western species, is locally abundant in Iowa and parts of Illinois, and bur ragweed, a Rocky Mountain species, occurs in western Iowa, but neither of these two latter species is considered important except possibly in restricted localities. Reaching into this region from the Southwest occurs

Table IV, HAYFEVER PLANTS OF THE NORTH-CENTRAL STATES: —

(Ohio, Kentucky, Indiana, Michigan, Illinois, Iowa, Eastern Missouri, Wisconsin and Southern Ontario)

SPECIES	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Acer saccharinum (Silver maple)												
Ulmus (Elms)												
Acer Negundo (Boxelder)												
Fraxinus americana (White ash).....												
Populus* (Poplars)												
Quercus (Oaks)												
Juglans nigra (Black walnut).....												
Carya (Hickories)												
Poa annua (Annual bluegrass).....												
Poa pratensis (June grass)												
Dactylis glomerata (Orchard grass)....												
Rumex Acetosella (Sorell dock).....												
Plantago lanceolata (English plantain)												
Poa compressa (Canada bluegrass) ...												
Lolium perenne (Perennial ryegrass)..												
Festuca (Fescue grasses)												
Phleum pratense (Timothy)												
Chenopodium album* (Lambsquarters)..												
Agrostis alba (Redtop)												
Amaranthus spinosus* (Spiny amaranth)												
Amaranthus retroflexus* (Pigweed) ...												
Cynodon Dactylon* (Bermuda grass)....												
Acnida tamarisc.* (West. waterhemp)..												
Chenopodium Botrys* (Jerusalem oak).												
Salsola Pestifer* (Russian thistle)....												
Cannabis sativa* (Hemp)												
Humulus Lupulus* (Hop)												
Helianthus annuus* (Sunflower).....												
Solidago (Goldenrods)												
Amb. psilostachya* (West. ragweed)....												
Artemisia caudata* (Wormwood).....												
Ambrosia trifida (Tall ragweed).....												
Ambrosia elatior (Short ragweed)....												
Amb. bidentata* (South. ragweed)....												
Cyclachaena xanthifolia* (Burweed)....												
Xanthium* (Cocklebur)												
Iva ciliata* (Marshelder)												
Artemisia annua* (Annual wormwood)												
Artemisia ludoviciana (Prairie sage)...												

* Discussed in the accompanying paragraphs.

western waterhemp. Its center of distribution is Oklahoma. In the north-central states it is regarded as an important factor in hayfever in many sections of Iowa, some of Illinois, and part of southern Indiana (BALYEAT and STEMEN 1927). Extending up from the South we find the southern ragweed including in its range almost the southern third of the north-central region, but, though frequently abundant enough to be a contributing factor in late-summer hayfever, its importance is largely overshadowed by the much more important short and tall ragweeds. Bermuda grass and spiny ama-

ranth, two important hayfever plants of southern regions, occur in the extreme southern part but are scarcely ever abundant enough to be very important.

Rough marshelder (*Iva ciliata*) occurs in the moist lowlands of the Mississippi and Ohio River valleys, and in East St. Louis and Cairo, Ill., it is said to be an important cause of hayfever. Hemp is common in northern Illinois, including Chicago, and sometimes associated with it is the hop. Both are of only doubtful significance in hayfever though they produce large amounts of anemophilous pollen. Sunflower is extremely abundant in some parts of the region and is probably a local factor of occasional importance. Cocklebur occurs throughout much of the region but is of relatively little importance. Of the chenopods, lambsquarters occurs practically everywhere and several other members of the genus as Jerusalem oak (*Chenopodium Botrys*), and the oak-leaved goosefoot (*C. glaucum* L.) are locally abundant but have little or nothing to do with hayfever.

The trees of this region appear to be less important than usual, only 7.3 per cent of the hayfever cases exhibiting symptoms from their pollen. The most important are ash, cottonwood, oak, maple and elm. Ash is common in the cities and it and several species of poplar or cottonwood, as the large-toothed aspen (*Populus grandidentata*), trembling aspen (*P. tremuloides*) and the necklace poplar (*P. deltoides*) are common and of some importance in the Chicago region. Several species of oak are also abundant there, though not actually in the city. Eastern sycamore (*Platanus occidentalis*) also occurs commonly in the region and is regarded as a possible cause of hayfever in Illinois. Species of willow and birch are also found but appear to be of little importance.

This region, comprising the north-central group of states and adjoining Canada, is so extensive that there may be considerable differences in the flowering periods of some of the plants in its southern and northern parts. The flowering of the trees and early grasses, the plants most affected by latitude, may be as much as two weeks earlier in the southern than in the northern part of the region, depending somewhat upon the season, while the late-flowering species, such as the ragweeds and goldenrods, may flower a little later in the southern than the northern part of the region. In other words, the summer season is longer in the southern part, starting earlier and ending later.

REFERENCES

The hayfever situation in most of the region of the north-central states has been adequately studied. HUBER (1926) recorded in tabular form all the hayfever plants of the region of Chicago and pointed out that *Cyclachaena* was abundant in certain sections while not in others, and that it appeared to be invading the city from all directions. Likewise he found that Russian thistle occurred abundantly enough in places to be included among his plants of primary importance, giving it a rating of 1 as compared with 4 for short ragweed. In his list of plants of secondary importance in the Chicago area are included bur ragweed, marshelder and cocklebur. HUBER also pointed out that, on account of the location of the city near Lake Huron and the peculiar topography of the surrounding terrain, the nature and severity of the hayfever was greatly influenced by wind direction and weather conditions. In the same year KOESSLER and DURHAM (1926) made a minutely detailed study of the hayfever situation in Chicago, dividing the city into blocks one mile square, each of which was studied separately. They found that 30 per cent of the city (40,000 acres) is allowed to run to weeds, largely ragweeds and hayfever grasses. They present in tabular form a pollen calendar of all the hayfever plants of the city and pollen counts of the most important species and show that the pollen of the ragweeds far outranked that of all others.

FEINBERG and DURHAM (1933) found that 93 per cent of the hayfever cases in this region suffered from ragweed pollen, 53 per cent from ragweed pollen uncomplicated by that of other species, the grasses accounted for 45 per cent of the cases, but of these only 6 per cent had their symptoms confined to the grass season. Slightly more than 7 per cent had definite hayfever from tree pollen, but of all such cases only one had symptoms confined to the tree season. Of the tree-sensitive cases 31 reacted to ash, 21 to cottonwood, 14 to oak, 14 to maple and 3 to elm. Definite reactions were obtained

in 32 cases to the pollen of Russian thistle, but in only a few of these was there reason to believe that this pollen was actually the major cause of their symptoms.

These investigators observed that in many places the dominant weed was *Cyclachaena*, and they made the very significant observation: "It is much more abundant now than it was eight years ago, but strangely enough has not become common except in the Chicago area". They also report that western waterhemp is common and increasing in the stockyard district but as yet is only a rare and local factor in hayfever. Among the grasses they find that June grass is the principal source of pollen, but Canada bluegrass is also an important contributor in the Chicago area. Among the trees, oaks, though not common in the city, occur abundantly near enough for their pollen to reach the city in considerable quantity. The tree-of-heaven (*Ailanthus altissima*) is commonly planted as a street tree and may be a minor factor in hayfever.

DURHAM (1933a) reports a survey of the whole of Illinois. He points out that the state lies in the midst of the ragweed continental area, where there are 6,000,000 acres of land devoted to the cultivation of wheat and small grains, and it is from these fields that the ragweed pollen comes, furnishing more than 95 per cent of the pollen in the air during the late-summer season. Cocklebur, he says, can not be of much importance though found throughout the state, but the annual and tall wormwoods (*Artemisia annua* and *A. caudata*) may be minor causes of hayfever.

FIGLEY (1926) furnishes a pollen calendar of all the hayfever plants believed to be important in Ohio, and he states: "In a city such as Toledo the pollen that causes its inhabitants hayfever comes from the grass and weeds of the vacant lots and is not as a rule blown in from the rural districts".

The hayfever situation of Indiana has been investigated by DURHAM (1929a, 1935a). In the former publication the author furnishes a pollen calendar and table showing the relative importance of the various hayfever plants. It is to be noted that among the 30 or more plants listed spiny amaranth, western waterhemp, southern ragweed and marshelder (*Iva ciliata*) are included but none of them ranked high in importance. In the latter publication DURHAM points out that ragweed constitutes 98 per cent of the atmospheric pollen in the fall, and that Indiana is one of the worst states of the country for ragweed.

A pollen survey for Ames, Iowa has been reported by COLES (1939). The situation there is not different from the rest of the region, but this author finds hemp and western waterhemp abundant enough to be important in hayfever, with *Kochia* rapidly encroaching on the area. Mold spores also occur in significant quantity. *Alternaria*, *Hormodendrum*, rust and smut spores were encountered abundantly.

The hayfever situation in Detroit has been investigated by WALDBOTT and STEERE (1931). The plants most commonly observed in the city were June grass, short ragweed, goldenrod and quack grass. "Burweed marshelder [*Cyclachaena*], redtop and Russian thistle were seen in such small numbers in the fields that they should be considered of local importance only".

These authors state: "In some of the outlying communities where the weeds [plants of giant ragweed] were mowed by the village authorities, it was noticed that several days following the cutting, new growth made the pollination as profuse as before". This observation draws forcibly to attention the futility of the methods at present in vogue in combating ragweed.

The hayfever situation in Ontario has been investigated by DURHAM (1933c), LARUSH (1934) and DETWEILER and HURST (1930). The reports of the first two of these investigations are valuable contributions to the literature of hayfever. DURHAM's report covers only the late-summer season, August 10 to September 30. He finds that, except in southern Ontario, the season is not long enough for the development of ragweed. In southern Ontario and Quebec he finds that the ragweed season begins about the middle of August, and by September 15 the air is almost free from the pollen. The ragweed pollen incidence at Toronto is about one third of that at Detroit and one eighth of that at Buffalo. Apparently virtually all of it comes from short ragweed; the giant is scarcely represented.

LARUSH has accomplished a most remarkable piece of work, reported as "The Pollen Content of the Air in Toronto, Canada". This is a daily record for one year

of atmospheric pollen caught on five slides exposed at each of seven different stations, that is to say 35 slides each day, together with "daily field observations from the time the early trees began to bloom until the first killing frost in the fall". Fifty eight different species of pollen were identified and counted on the slides, the identifications being made on the basis of their morphology checked by the record of the flowering of the plants in the field. Among the trees recorded are silver maple (April 2 to 11), red maple (April 15 to May 1), elm (April 21 to May 10), poplar (May 4 to 15), birch (May 11 to 29), oak (May 26 to June 11), ash (May 13 to 27), boxelder (May 7 to 15). Of these the pollen counts of oak, elm and birch greatly outnumbered the others. Among the grasses recorded are June grass (June 8 to 19), but the grass pollen curve shows that it reaches effective quantities toward the first of June rapidly rising to its peak on June 19, and falling off with wide daily fluctuations to the end of September. Among the weeds recorded are plantain (July 4 to Aug. 20), *Chenopodiaceae* (July 14 to September 18), *Artemisia biennis* (August 26 to November 1), *Artemisia caudata* (August 7 to 24), short ragweed (August 16 to October 1). The pollen of the latter enormously outnumbers that of all others. The curve shows that ragweed pollen in Toronto reaches effective quantity about August 15, rises rapidly to its peak at about September 5, thereafter declining at first rapidly then slowly to the end of the month. An examination of LARUSH's tables shows at a glance the complete story of practically every kind of pollen in the air, and the enormous number of observations upon which these tables are based is a guarantee of their accuracy. One leaves this remarkable report with a sigh of regret that there are not more such, and that death cut prematurely short so promising a career as that of its author.

GROH and MINSHALL (1940), reporting on the ragweed situation in eastern Canada, state that the peak incidence of short ragweed pollen is found in Montreal and the region around the southern tip of Lake Ontario, while the northern parts of Ontario and Quebec are nearly free. The Gaspé peninsula is free and the Quebec Department of Agriculture is making a determined effort to keep it so. In Nova Scotia the authors find the rich agricultural region of the Annapolis Valley to be heavily infested with ragweed.

The hayfever situation of the North Central Region, and the literature pertaining to it have been briefly but effectively summarized by HANSEL (1936) and VAUGHAN (1931, 1939) and more fully by DURHAM (FEINBERG 1934) together with additional observations by these investigators not previously reported.

FASSETT, MCGARY and BATES (1938) have compiled a sort of atlas of what are stated to be the hayfever plants of Minnesota, Wisconsin, Iowa, Illinois, Missouri and Indiana, showing by maps their distribution within these states. The figures are largely reproductions from standard botanical texts and the maps are compilations from similar sources. Their conclusions, they state, are based on THOMMEN's five postulates and "the results of tests made on more than 600 pollen sensitive cases".

V. The Southern States (Florida, Tennessee, Georgia, Alabama, Mississippi, Louisiana, Arkansas, Southern Missouri, Oklahoma and Eastern Texas) :—

Juniperus. — Mountain cedar (*J. mexicana*) occurs only on the limestone hills of Texas, but is especially abundant in the neighborhood of Austin and Dallas where it has proved to be one of the most important hayfever plants, accounting for hundreds of cases of midwinter hayfever. Other species of juniper also occur in the southern area; the red cedar (*J. virginiana*) is abundant, reaching its maximum development in the "Cedar Glades" of Tennessee and northern Alabama.

Corylus. — Two species of hazel (*C. americana* and *C. rostrata*) are abundant locally, the latter especially in the mountains of Georgia.

Populus. — Several species of cottonwood or poplar, including *P. del-*

toides and *P. alba*, are abundant and have been recorded as important in Memphis, parts of Alabama and San Antonio.

Betula. — The principal birch of the South is the red or river birch (*B. nigra*) extending almost throughout the region, from Florida to eastern Texas. *B. lenta* is also found in the northern part.

Quercus. — Many species of oak occur, and in most places they are the commonest trees, contributing the greater part of all the tree pollen. One of the commonest is the live oak (*Q. virginiana*) extending almost throughout the South, but especially characteristic of Texas where it is regarded as one of the most important hayfever trees (KAHN and GROTHAUS 1930). The black-jack oak (*Q. marilandica*) is the most abundant tree of Oklahoma but is there regarded as only a minor cause of hayfever. *Q. alba* and *Q. rubra* are considered to be important in Alabama (WEIL 1931, 1937). Most oaks are so closely related that their pollens are generally regarded as interchangeable, but KAHN and GROTHAUS (1930) state: "Live oak has been our local factor, the other oaks of our community [San Antonio] often giving negative skin tests in our positive oak cases".

Carya. — Several species of hickory are common throughout the South but by far the most important is pecan. It is especially abundant in the southern part of Georgia, Alabama and Mississippi where it is frequently the cause of a very severe type of hayfever. *C. ovata*, *C. laciniosa* Loud., *C. glabra* and *C. alba* also occur in various parts of the South.

Tricholaena rosea. — Natal grass is abundant in parts of Florida and occurs sparingly at other places in the Gulf states but is of little or no importance in hayfever.

Ligustrum. — The privets are undoubtedly an important factor in hayfever and are reported as such in New Orleans (THIBERGE 1934). Several species are involved. See p. 121.

Phleum and *Dactylis*. — Timothy and orchard grass occur only in the northern part of the region. For example in Memphis and vicinity where both are reported as important (LACKEY and GOLTMAN 1934).

Amaranthus. — Carelessweed is found in quantity only in southern Texas where it is regarded as moderately important. Of probably greater importance is the spiny amaranth. In the northern part of the region it blooms from June to August or September, but in the southern part, as at New Orleans, it blooms practically throughout the year. HEINBERG (1930) has shown that in Florida (Pensacola) it may be the sole cause of a severe type of hayfever. In many other parts of the South it is probably a contributory cause of considerable importance. It is mentioned in Alabama as such (WEIL 1931), the Gulf states (SCHEPPEGRELL 1916a), and in New Orleans (PENFOUND, EFRON and MORRISON 1930). *Amaranthus retroflexus* and *A. hybridus* are common practically throughout the southern area but are unimportant.

Acnida tamariscina. — Western waterhemp is one of the most important plants in Oklahoma and adjacent part of Texas (BALYEAT and STEMEN 1927) but outside of this region is scarcely anywhere abundant enough to be a factor in hayfever.

Table V, HAYFEVER PLANTS OF THE SOUTHERN STATES:—

(Tennessee, Georgia, Florida, Alabama, Mississippi, Louisiana, Arkansas, Southern Missouri, Oklahoma and Eastern Texas)

SPECIES	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Juniperus mexicana* (Mountain cedar)												
Juniperus virginiana* (Red cedar).....												
Alnus rugosa (Smooth alder)												
Ulmus alata (Winged elm)												
Ulmus americana (White elm).....												
Corylus* (Hazel)												
Taxodium distichum (Bald cypress)....												
Populus* (Poplars, Cottonwoods).....												
Acer (Maples)												
Acer Negundo (Boxelder)												
Betula nigra (Red birch).....												
Betula* (Birches)												
Quercus* (Oaks)												
Salix (Willows)												
Morus (Mulberries)												
Maclura pomifera (Osage orange).....												
Celtis laevigata (Southern hackberry)..												
Liquidambar styraciflua (Sweetgum)....												
Platanus occidentalis (Sycamore).....												
Fraxinus americana (White ash)												
Carya Pecan (Pecan)												
Carya* (Hickories)												
Juglans nigra (Black walnut).....												
Poa pratensis (June grass)												
Paspalum dilitatum (Dallis grass).....												
Tricholaena rosea* (Natal grass)												
Plantago lanceolata (English plantain)												
Rumex acetosella (Sorrel dock)												
Ligustrum* (Privets)												
Broussonet. papyrif. (Paper mulberry)..												
Lolium perenne (Perennial ryegrass)....												
Lolium multiflorum (Wintergrass).....												
Dactylis glomerata* (Orchard grass)....												
Festuca octoflora (Six-weeks fescue)....												
Cynodon Dactylon (Bermuda grass).....												
Phleum pratense* (Timothy)												
Sorghum halepense (Johnson grass)....												
Amaranthus spinosus* (Spiny amaranth)												
Amaranthus retroflexus* (Pigweed)....												
Amaranthus Palmeri* (Carelessweed)..												
Acnida tamarisc. (West. waterhemp)....												
Chenopodium album (Lambsquarters)....												
Chenopodium ambrosioides (Mex. tea)..												
Chenopodium Botrys (Jerusalem oak)....												
Agrostis alba (Redtop)												
Amb. psilostachya* (West. ragweed)..												
Ambrosia bidentata* (Southern ragweed)												
Ambrosia trifida (Tall ragweed)												
Ambrosia elatior (Short ragweed).....												
Ambrosia hispida (Seashore ragweed)..												
Ambrosia aptera (West. giant ragweed)												
Cyclachaena xanthifolia* (Burweed)....												
Xanthium speciosum* (Great clotbur)..												
Xanthium* (Cocklebur).....												
Iva frutescens* (Common marshelder)..												
Iva ciliata* (Rough marshelder).....												
Iva angustifolia (Marshelder).....												
Artemisia annua* (Annual wormwood)....												

* Discussed in the accompanying paragraphs.

Table V. — Concluded: —

SPECIES	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
<i>Salsola Pestifer</i> * (Russian thistle).....												
<i>Ulmus serotina</i> * (September elm).....												
<i>Ulmus crassifolia</i> * (Cedar elm).....												
<i>Sorghastrum nutans</i> * (Indian grass)....												
<i>Baccharis halimifolia</i> * (Groundsel bush)												
<i>Casuarina</i> * (Australian pine)												

* Discussed in the accompanying paragraphs.

Ambrosia. — The two principal ragweeds, as in the eastern states, are the tall and short. The former is found almost throughout the eastern part of the southern area but does not extend in effective quantity west of Oklahoma City. In the extreme southern part of the area, as in parts of Florida and New Orleans, the plants flower almost all summer, starting in May or earlier, but they shed much less pollen than in the East. Tall ragweed is not found in Florida nor the southern part of Georgia and Alabama, and from the Mississippi valley westward is largely replaced by the Texas great ragweed (*A. aptera*). Southern ragweed occurs on the prairies and interior low plateaus from western Mississippi and Tennessee westward including Arkansas and Oklahoma. Western ragweed is found from the Mississippi River westward but is not important except in western Oklahoma and the southernmost part of Texas (DURHAM 1933b).

Cyclachaena. — Prairie ragweed "is found in the South principally in the panhandle of Oklahoma, in Texas and the northern corner of Missouri" (DAVISON, LOWANCE and DURHAM 1934). It is also recorded in Arkansas (LACKEY and GOLTMAN 1934).

Xanthium. — Various species of cocklebur are common throughout the region but for the most part they are unimportant. The great clotbur (*X. speciosum*), however, sheds much more pollen than most species and is common in the Mississippi valley and westward.

Iva. — Rough marshelder is found almost throughout the South from the western part of Georgia westward. Narrow-leaved marshelder is found in Arkansas, Oklahoma and Texas. In southern Oklahoma and eastern Texas it is regarded as an important local factor in hayfever (DAVISON, LOWANCE and DURHAM 1934). *I. frutescens* grows only in the tidal marshes along the coast. In such places it may occasionally be a minor local factor in hayfever.

Artemisia. — The mugworts and wormwoods are of relatively little importance in the southern area, though several species occur. *A. annua* is found in most places, exclusive of Oklahoma, Louisiana and Texas, and *A. vulgaris* occurs fairly abundantly in parts of Alabama and Georgia.

Salsola. — Russian thistle occurs in appreciable quantity only in Oklahoma and adjacent parts of Texas.

Ulmus. — Scrub or cedar elm (*U. crassifolia*) occurs from Mississippi to central Texas. Flowering at about the same time as the ragweeds, it occasionally complicates late-summer hayfever. September elm (*U. serotina*) occurs in Georgia, Alabama and Tennessee but appears to be rarely common enough to be of any importance (BLACK and DURHAM 1930).

Sorghastrum nutans. — Indian grass is found in dry places throughout the South, and in the prairie regions of the Mississippi valley it was formerly one of the most important tall prairie grasses but its numbers have been decimated through agricultural operations. It is probably much less harmful than the weeds that have largely taken its place, but it is regarded as having hayfever possibilities in Florida (NICHOL and DURHAM 1931) and elsewhere by other investigators.

Baccharis halimifolia. — Groundsel bush occurs along the coast from Florida to Texas and is particularly abundant in parts of Florida where it is regarded by NICHOL and DURHAM (1931) as a possible cause of hayfever.

Broussonetia papyrifera. — Paper mulberry appears to be a local cause of hayfever as far west as Oklahoma and Texas (BALYEAT and RINKEL 1932).

Casuarina. — Several species of Australian pine are extensively planted in Florida especially along the beaches and water ways as sand binders. *C. Cunninghamia* is particularly abundant in and around St. Petersburg and Tampa, where it flowers in September and October. Though its pollen has marked hayfever characteristics it is reported by METZGER (1939) to be of no importance in hayfever. On the other hand ZIVITZ (1942) states that in the region of Miami, where *C. equisetifolia* and *C. lepidifolia* are abundant, their pollen does cause some hayfever. On the Gulf coast the casuarinas flower profusely in September and October. But on the east coast they are reported to flower in March, April and December.

REFERENCES

Much excellent work has been done to discover the causes of hayfever in the South, but the problem is extremely complicated by the size of the region and the variety of conditions encountered. Most of the studies are local, dealing with single states, parts of states or single cities. But WODEHOUSE (1941) gives a general discussion of the hayfever situation in the South. DAVISON, LOWANCE and DURHAM (1934) have made a study of the huge southern area "which reaches from the lower borders of Pennsylvania and New Jersey on the north to the Florida keys and from Chesapeake Bay and Cumberland Sound on the east to the western part of Texas".

Also of general application is the report by DURHAM (1933b) on the ragweed situation in the Southern states. He finds that the only ragweeds of major importance are the tall and short.

Oklahoma. — BALYEAT through surveys of the Oklahoma flora in association with T. R. STEMEN finds that the trees are relatively unimportant, the commonest being the necklace poplar (*Populus deltoides*) flowering from April 5 to 26, and black-jack oak (*Quercus marilandica*) April 15 to May 1, the latter the commonest tree in the state. The grasses are principally Bermuda and Johnson grass. Among the weeds Russian thistle, lambsquarters and pigweed are found to be abundant, but of much greater importance is western waterhemp. Tall, short and western ragweeds they find to be accountable at least partly for about 73 per cent of all cases. Minor causes are considered to be rough marshelder, cocklebur, corn, and gray sage (*Artemisia Wrightii*).

A detailed study of the hayfever plants of Tulsa county and adjoining territory of Oklahoma is reported by DENNY and TENNY (1932).

Alabama.— The hayfever situation in Alabama has been extensively studied by WEIL (1931, 1937). In the earlier report is furnished a pollen calendar prepared especially for Montgomery but designed to apply more or less exactly to the whole state, and in the latter is furnished a complete list of Alabama plants which have hayfever possibilities. WEIL states that he is convinced that there are hundreds of cases of pecan hayfever in Alabama that: "Patients who are sensitive to pecan pollen usually have symptoms at least as severe as those due to ragweed pollen and frequently more severe. Half of the cases had asthma as well as hayfever". The pollen is found in the air from the middle of April to the latter part of May. Hickory and black walnut are also important, but their pollens interact with each other and with that of pecan so that "immunization against one will protect against all three."

Among the grasses WEIL finds the most important to be rye grass, Bermuda grass and Johnson grass, but only half of the summer cases occurring between May and September were found to be due to grass pollen, the others being due to some as yet unknown cause.

Late-summer hayfever, occurring from September 1 to frost, was found to be due almost entirely to tall and short ragweed with cocklebur a minor contributing factor. Spiny amaranth is also considered to be a factor at this time, since it is abundant in the region and flowers at about the same time as the ragweeds and about 40 per cent of the hayfever patients react to its pollen.

Tennessee.— SPRITZ (1927) and BOWIE (1939) reporting from Nashville, point out that hayfever occurs there in three seasons. The early-spring season extends from about the end of February to the middle of May and is due to cottonwood walnut, birch, elm, maple, willow and "cedar"; the summer hayfever season extends from the middle of April to the end of summer, and is due to the pollen of grasses of various kind, including Bermuda and Johnson grass; and the late-summer hayfever season extends from the end of July to frost and is due almost entirely to the ragweeds.

HENRY and HERRING (1930) have furnished a botanical survey of Memphis and surrounding territory within a radius of 200 miles. This area includes the eastern end of Tennessee and adjacent corners of Kentucky, Mississippi, Arkansas and Missouri. For this region the authors list, with their times of flowering, some 80 species of plants with hayfever possibilities. They point out that Russian thistle does not occur in this region.

HENRY (KAHN and GROTHAUS 1930) gives an abbreviated list of the more important hayfever plants of Memphis, stating that probably the most abundant tree of the region is oak, and that the first trees to flower in spring are the elms starting about the first week in February.

LACKEY and GOLTMAN (1934) in a hayfever survey of the Memphis area list, with their flowering periods, about 90 species which might be suspected of causing hayfever. They point out that a large variety of plants is encouraged by the geographical variety of the region, comprising the delta, loess bluffs and north central plateau, all presenting widely different natural floras. However, the dominant flora existing at present throughout most of the region is so much the result of human interference that natural ecological factors are less important than would otherwise seem.

Louisiana.— Almost the earliest work done in the United States on the botanical aspect of hayfever was that of SCHEPPEGRELL (1916a, 1916b) at New Orleans. Later this work was extended to include the whole of the United States and published by SCHEPPEGRELL (1922) in his book on Hayfever and Asthma, but these pioneer works are now mainly of historical interest.

A study of the hayfever situation in New Orleans has more recently been made by PENFOUND, EFRON and MORRISON (1930). They say that the city presents the maximum of hayfever and asthma hazard because of the long and favorable growing season and because approximately 70 per cent of the land is abandoned to weeds. There is so little frost, occurring only from December 7 to February 14, that allergic diseases due to pollen may exist throughout the year. The maximum for most cases, however, oc-

curs from July to September. Their report of a botanical survey of the city of New Orleans and some of the surrounding suburbs lists with their relative abundance about 60 species of weeds exclusive of trees, which are known to cause hayfever or have hayfever possibilities. New Orleans is predominantly a region of grasses, the commonest being Bermuda grass with a flowering period from April to December, and it constitutes the greatest hazard in pollen allergy. Also extremely abundant are two species of *Paspalum* known as bull grasses, *P. dilatatum*, tall bull grass or Dallis grass, and *P. Vaseyanum*, hairy bull grass, both flowering from April to November. Also important is the tall ragweed, flowering from July to December and to a lesser extent short ragweed flowering at about the same time. The pollinating periods of many hayfever plants in New Orleans are variable depending upon weather and human influences such as cutting of grass and weeds, and soil disturbances. "It is recognized also that perhaps 40 per cent of the species may, during years of favorable conditions, bloom throughout the entire year". Consequently hayfever does not fall into well marked seasons as it does farther north. Some of the hayfever plants can be classed as winter bloomers, spring bloomers, autumn bloomers and ever bloomers. The most important are the latter, effective from early April to December.

THIBERGE and HAUSER (1931) present a list of common plants with hayfever possibilities showing their time of flowering, distribution and the size and shape of their pollen grains. This study, however, does not apply especially to the plants of Louisiana, though reported from New Orleans, but is rather of nation wide scope. The authors draw attention to an interesting case of *Clematis* hayfever discovered by finding pollen grains on slides exposed in the patient's sleeping room. In a later paper THIBERGE (1934), in discussing trees suitable for planting in the South, points out that several species of privet, as they are commonly grown there, permitting the plants to go untrimmed and bear flowers, are important causes of hayfever.

Florida. — NICHOL and DURHAM (1931) report the result of a botanical survey and the daily record of pollen caught on oiled slides at Miami over a period of two years. They record unusually low pollen counts which they attribute to the lack of extensive agricultural areas and to the fact that the prevailing winds during the summer and fall are from the ocean. The authors also furnish a list of the wind pollinated plants of Miami with their dates of flowering. It is interesting to notice that some of these, as cocklebur and the palms, are not represented at all in the pollen record, and others, as pine and oak, are only poorly represented in spite of their abundance in the vicinity. This suggests that the prevailing ocean breeze is the principal determining factor in the low pollen incidence.

The grasses in Florida are believed by NICHOL and DURHAM to be the principal cause of what little hayfever there is. Bermuda and Natal grass are suggested as the most important, flowering throughout the year except January and part of February. Next in importance they consider to be Johnson grass with a flowering period almost as long. There is no giant ragweed but the dwarf ragweed flowers from May to October. Ragweed plants on account of their long growing season reach abnormally large proportions but shed relatively little pollen. As a result of their studies they conclude that: "The sea coast of Florida is just about as nearly perfect for ragweed hayfever sufferers as any place could be".

METZGER (1932, 1939) finds that, while the beaches of the east coast of Florida may be essentially free from ragweed pollen, this is unhappily not true of the west coast. Sarasota, Arcadia and Tampa, he finds, have sufficient ragweed to cause trouble. "The west coast of Florida is now undergoing the sad experience that many of the Michigan hayfever resorts had . . . Since I have become weed conscious, I notice each year a definite increase in ragweed".

Eastern Texas. — The earliest contribution to our knowledge of hayfever in Texas to be found in the literature is that of KEY (1918). He reported the cause of winter hayfever, which makes its appearance between the middle of December and Christmas and lasts until the middle of February, to be the pollen of mountain cedar. The extraordinary prevalence of this type of hayfever in the parts of Texas where the cedar grows is the outstanding characteristic of hayfever in Texas.

HULSEY (1933) reporting from Fort Worth, records the atmospheric pollen counts over a period of three successive years, showing mountain cedar from December 9 to February 1, elm from March 1 to May 5 and again in September and October, cottonwood from March 15 to April 15, Oak from March 21 to May 1, ragweed from September 1 to November 10, and grass pollen occurring in small amounts all through the year. There is found, however, considerable variation in the flowering periods from year to year, mountain cedar pollen sometimes being caught as early as November 4 and ragweed as late as December 31, and both causing symptoms of hayfever.

KAHN and GROTHAUS (1930) in their study of tree-pollen hayfever in the South find that "The tree pollen causing the largest amount of distress in any of the southern states is that of the mountain cedar. Its annual victims can be numbered by the thousand". Otherwise they find that pure tree-pollen hayfever is very rare. But tree pollen complicating hayfever of other origin is much commoner, often severe and generally multiple. In San Antonio the most important trees they found to be pecan, flowering from March 30 to May 9, and live oak, from March 9 to May 6. Others of considerable importance are ash, cottonwood, willow, several species of oak, hackberry, boxelder and sycamore and, in Dallas, elm. KAHN (1924, 1926) reports the results of exposing atmospheric pollen slides. "The process", he says, "is exceedingly satisfactory and no more difficult than the examination of an ordinary microscopical urinary sediment". He finds that in San Antonio grass pollen remains in the air practically throughout the year, though never in very large amounts. Still it is sufficient to make grass hayfever perennial. The amaranths, carelessweed and pigweed, are important in southern Texas rather than the ragweeds during the late summer. The ragweeds, *Ambrosia trifida* and *A. psilostachya*, they find "are moderately profuse but owing to the dry months of late July and August, they do not pollinate to any extent until the middle of September". But during this period ragweed pollen in southern Texas never exceeds that of the grasses, though in northern Texas the reverse is true.

FRENCH (1930) reporting from Fort Sam Houston, finds that the principal causes of hayfever are Bermuda grass, Johnson grass, tall ragweed, short ragweed, pigweed, carelessweed, plantain and mountain cedar, the latter being a frequent cause indoors when used as Christmas trees.

Summer Hayfever of Unknown Origin:—In spite of the unusually large number of pollens which have been shown, or suspected, to cause hayfever in the South, probably more than half of the summer hayfever cases still remain unexplained. WEIL (1937) reports from Alabama that out of a group of 22 cases of summer hayfever 12 failed to react to pollen or any other allergen with which he tested them, and when treated with grass pollen, as non-reactors, failed to be benefited. He states: "It must be admitted that we do not yet know the cause of over half of the cases occurring in the summer months." Later WEIL (1940) reports the study of 47 such cases occurring between May and September or October.

Allergists have lately come to recognize this type of hayfever as a definite entity peculiar to the South caused by an unknown factor—or possibly several unknown factors, hence it is called "Summer Hayfever of Unknown Origin" or more recently, "X hayfever". The symptoms are characteristic of hayfever and asthma caused by pollens. They begin usually in May and persist throughout the summer, gradually tapering off toward the end of September or the beginning of October. There is diurnal variation in the symptoms; most cases are worse at night and early morning, often nearly or quite free in the afternoon. Some patients maintain a degree of freedom by remaining in an air conditioned room while others are not benefited at all by air conditioning, finding themselves worse indoors than out. All are immediately relieved by leaving the infested area, generally going to the coastal beaches.

In an endeavor to discover the distribution and prevalence of X hayfever both EFRON and the present writer sent out questionnaires to all of the allergists of the South who could be contacted. To both the responses were most gratifying. According to the answers received the distribution of X hayfever approximately coincides with the southern coastal plain with a northward extension along the Mississippi delta to the southwestern tip of Kentucky. Roughly this includes the southern part of South

Carolina, the southern two thirds of Georgia and Alabama, northern Florida, the western tip of Tennessee, Mississippi, Louisiana, and southeastern Texas. The questionnaire also brought out the fact that X hayfever is more prevalent in the southern reaches of this area than in the northern, reaching a maximum of 65 per cent of all hayfever cases in New Orleans.

So important and so baffling has proved the problem of X hayfever that a group of allergists of the South has formed itself into the Committee of Allergists for the Study of the Unknown Causes of Hayfever (BOWEN 1941). The Committee is headed by RALPH BOWEN of Houston, Chairman, and B. G. EFRON of New Orleans, Secretary. In announcing the formation of the Committee BOWEN states that the following are not of etiological importance: "1. Pollens, 2. Johnson smut, 3. Air borne fungus spores that are readily cultured on artificial media; such as *Alternaria*, *Hormodendrum*, *Aspergillus*, etc. . . . The Committee welcomes corresponding members".

Further activities of the Committee are reported by EFRON (1942-1943). They have investigated the possibility of insect emanations as the cause of X hayfever, testing cases with extracts of 17 different insects, including such as the large American roach which is extraordinarily abundant in the South, the citrus white fly, midge and others which occur in the infested area. Positive skin tests were obtained from the insect allergens with 25 per cent of the X-allergic cases tested. However, the reactions were not specific; those individuals who reacted to one insect reacted to the others. And since the incidence was lower than would be expected, and insects are ubiquitous, they are not to be considered the answer to the X hayfever problem. So this line of attack is to be abandoned by the Committee.

A later report from the Committee of Allergists for the Study of Unknown Causes of Hayfever (1943) shows a return to the unfinished investigation of fungus spores as a possible cause of X hayfever. The spores were collected from infected air by means of the Wells air centrifuge and picked directly from the celluloid strips by means of a micromanipulator and grown as single spore cultures. Others were washed off with sterile distilled water and plated out in the usual way. Cultures were grown on potato-dextrose agar. Extracts made from the pellicles obtained from 10 species of fungi were tested on X-hayfever cases. Positive skin reactions comparable in size with those obtained from pollen extracts with hayfever cases, were obtained with extracts of *Fusarium*, *Helminthosporium*, *Cladosporium*, *Trichoderma* and *Alternaria*. The Committee concludes, however, that: "Although it is apparent that these molds are not the etiologic agents responsible for X hayfever and asthma, further investigation of fungi is justified by the data already obtained." From the work of such an active and determined group of investigators as this Committee of Allergists, there is good reason to hope that the etiologic factor of X hayfever will eventually be discovered.

Fungi:—There is no doubt that mold spores play an important part in asthma and hayfever of the South, though perhaps not more so than elsewhere. PRINCE, SELLE and MORROW (1934) and PRINCE and MORROW (1937) have shown that mold sensitizations in Galveston are more likely to be manifest in the winter months, and "an increase in the mold content of the air is actually encountered in the winter when the moisture is conducive to the growth of fungi". These authors have shown that when the wind blows from the north and northeast the count of mold spores at Galveston greatly increases, and when the wind blows off the Gulf the spore count drops almost to zero. This they attribute to the extensive marsh land to the north and northeast of the island. They found many hayfever and asthma patients sensitive to such forms as *Monilia*, *Penicillium*, *Aspergillus*, *Trichoderma*, *Helminthosporium*, *Hormodendrum*, *Cladosporium* and some unidentified species. And treatment with extracts of these proved satisfactory in most cases.

Encouraged by these results a group of allergists formed themselves into the Association of Allergists for Mycological Investigations, for the purpose of extending these investigations to include air-borne molds in central and southwestern United States. The first report of the Association has been published by MORROW, LOWE and PRINCE (1942). It deals with the atmospheric mold spores from widely separated stations, including El Paso, Abilene, Fort Worth, Dallas, Waco, Temple, San Antonio, Houston

and Galveston in Texas; Shreveport in Louisiana; Little Rock in Arkansas; Nashville in Tennessee; St. Louis and Kansas City in Missouri; Minneapolis in Minnesota; Milwaukee in Wisconsin; Evanston in Illinois; and Toledo in Ohio. At each of the stations agar plates were exposed at semimonthly intervals. The molds which could be cultured from these were identified by experts in the groups to which they belong. In addition to those species recorded for Galveston, such forms as *Alternaria*, *Spondyli-cladium*, *Fusarium*, *Mucorales* and *Pullularia* were prominent. The dominant forms were found to be *Alternaria* and *Hormodendrum*, occurring more frequently and in higher numbers than any other molds and reaching their maxima in the winter months. *Aspergillus* and *Penicillium* also occurred frequently but more or less uniformly throughout the year. *Pullularia* when present occurred as a "shower" making up the major part of the total count for the station.

These investigators found no significant differences between the northern and southern stations which could throw light on the X hayfever of the South. In fact the spore counts from the northern stations were even higher than those from the southern.

The Association is continuing its work and promises an early report of further results.

Hayfever Resorts:—Most hayfever sufferers are able to secure a measure of relief by going to the mountains of northern Georgia and the Carolinas, or to the beaches. EFRON (1942-1943) lists Savannah, Brunswick and Jacksonville beaches, Panama City, Biloxi, Gulfport, Pass Christian and Galveston as short resorts at which patients with X hayfever may find relief. These are likewise credited as resorts for victims of hayfever from ragweed and other pollen. For the most part the beaches owe their comparative freedom from pollen to the fact that the wind at these places generally blows off the ocean. Their chances of freedom are much greater when the resorts are well separated from the mainland by intervening water or marsh land, which is often the case.

In Georgia both Savannah and Brunswick beaches offer partial or complete relief from pollen and X hayfever. In Florida, Jacksonville Beach offers a measure of relief but some patients who find themselves benefited at Savannah Beach have reported no benefit at Jacksonville Beach. This is probably because the extensive areas of marsh land originally separating the beach from the mainland have now been largely filled in and bear a flourishing crop of weeds. Most of the beaches along the east coast of Florida can justly claim a high degree of immunity. Miami Beach appears to be virtually free from hayfever pollen. This is because the wind here nearly always blows off the ocean and the beach is well separated from the mainland by a large inlet from Biscayne Bay. Places close by on the mainland, such as Miami and Coral Gables are by no means free from hayfever on account of the large weedy areas surrounding them. Key West can quite justly claim almost complete immunity from hayfever. This, however, is entirely due to its insular position, for ragweed can be found flourishing in and around the city itself. But being an island Key West always has a sea breeze.

Panama City claims a degree of freedom from hayfever, especially that of the X type. Such immunity that it possesses, however, is largely due to the fact that the prevailing winds are from the Gulf, and much of the region to the landward of the City is open water and marsh land. The City itself has an abundance of vacant lots fully occupied by short ragweed and other hayfever weeds. Pensacola can not be regarded at all favorably as a hayfever resort. It is one of the weediest cities on the Gulf Coast.

In Mississippi Biloxi, Gulfport and Pass Christian all claim a high degree of immunity from hayfever of both the X and the recognized pollen types. Biloxi is perhaps the best situated since it is separated from the mainland by considerable open water and marsh land, but in the main these resorts depend upon the breezes from the Gulf to keep them supplied with pollen-free air since they themselves are badly infested with hayfever weeds.

Galveston claims a degree of immunity from both the X and recognized pollen types of hayfever owing to the fact that it is an island and largely supplied with pollen-free air from the Gulf.

VI. The Southwest (Arizona, New Mexico, Western Texas):—

Hayfever in the Southwest is more severe and more complicated than in most other regions. It is also more of a local problem. The settlements

Table VI, HAYFEVER PLANTS OF THE SOUTHWEST:—
(Arizona, New Mexico, Western Texas)

SPECIES	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Juniperus mexicana* (Mountain cedar).....												
Juniperus* (junipers).....												
Populus* (Cottonwoods).....												
Fraxinus Toumeyii* (Arizona ash).....												
Quercus* (Oaks).....												
Olea europaea (Olive).....												
Prosopis juliflora* (Mesquite).....												
Lolium perenne (Perennial ryegrass)...												
Bromus* (Brome grasses).....												
Cynodon Dactylon* (Bermuda grass)....												
Sorghum halepense (Johnson grass).....												
Distichlis spicata* (Salt grass).....												
Poa pratensis* (June grass).....												
Bouteloua* (Grama grasses).....												
Chloris virgata* (Finger grass).....												
Agropyron Smithii (Bluestem).....												
Koeleria cristata (Western Junegrass)...												
Amaranthus retroflexus (Pigweed).....												
Amaranthus spinosus* (Spiny amaranth)												
Amaranthus Palmeri* (Carelessweed) ..												
Amaranthus gracizans* (Tumbleweed)												
Acnida tamarisc. (West. waterhemp)...												
Chenopodium album (Lambsquarters)...												
Atriplex Wrightii (Annual saltbush)....												
Atriplex canescens (Wingscale).....												
Atriplex* (Saltbushes).....												
Salsola Pestifer* (Russian thistle).....												
Kochia scoparia* (Burningbush).....												
Kochia americana (Redsage).....												
Allenrolfia occidentalis (Burroweed)....												
Helianthus annuus (Sunflower).....												
Artemisia tridentata* (Sagebrush).....												
Artemisia filifolia (Silvery wormwood)...												
Artemisia dracunculoides (Dragon sage)												
Artemisia gnaphalodes (Prairie sage)...												
Artemisia Wrightii (Gray sage).....												
Artemisia Bigelovii (Dwarf sagebrush)...												
Artemisia canporum (Field sawewort)...												
Artemisia frigida (Pasture sage).....												
Ambrosia psilostach. (West. ragweed)												
Ambrosia aptera (West. giant ragweed)												
Franseria ambrosi. (Canyon ragweed)...												
Franseria deltoidea (Rabbit bush).....												
Franseria dumosa (Bush sandbur).....												
Franseria discolor (Low ragweed).....												
Franseria acanthicarpa (Bur ragweed)...												
Franseria tenuifolia (Slender ragweed)...												
Hymenoclea Salsola* (Greasebush)....												
Hymenoclea monogyra (Jecote).....												
Dicoria Brandegei (Dicoria).....												
Dicoria canescens (Dicoria).....												
Iva axillaris (Povertyweed).....												
Cyclachaena xanthifolia* (Burweed)...												
Xanthium (Cocklebur).....												

* Discussed in the paragraphs immediately following.

of the arid regions generally owe their existence to irrigation, which presents conditions favorable to the growth of hayfever plants. Within relatively short distances widely varying types of flora may be encountered owing to differences in elevation as well as to conditions of irrigation. Moreover the dry atmosphere which prevails throughout most of the region favors pollination by wind, resulting in a greater proportion of the vegetation being anemophilous than is encountered in regions of heavier rainfall. WILSON (1934) has found a large proportion of the victims of hayfever—much larger than in most other regions—to show no family history of allergic manifestations, from which it is to be inferred that the atmospheric conditions are such that persons in this region, even without predisposing causes, may easily fall victim to hayfever.

Hayfever Seasons:—The division of the year into three hayfever seasons does not apply at all strictly here. It is true that three seasons corresponding to those of the East may be recognized to some extent but a fourth in midsummer is added, due to the chenopods and amaranths which are here much more important than the ragweeds; and in Arizona three of the false ragweeds, which are allergenically similar to the true ragweeds, flower early in spring, making really two ragweed seasons. Besides this, Bermuda grass, which is by far the most important hayfever grass if, indeed, not the most important of all causes of hayfever, throughout nearly the entire region, flowers at irregular and unpredictable intervals nearly all year round, for it depends much more upon rainfall and irrigation for its flowering than upon the cycle of the seasons. Also in western Texas the mountain cedar which is one of the most important causes of hayfever in this region, flowers in mid-winter. So, to speak of hayfever in the Southwest by seasons loses its meaning; it is hayfever season all the time.

The Trees

Poplars.—The commonest and most important of the poplars is the Arizona cottonwood (*Populus McDougallii*) growing naturally throughout much of the region and commonly planted in the irrigated valleys. Several other species are also common. The valley cottonwood (*P. Wislizenii*) is perhaps the best known tree of New Mexico where it is extensively used as a shade tree. It is also common in Arizona where it is counted as a cause of hayfever of secondary importance. The mountain cottonwood (*P. angustifolia*) is common in all the mountains of New Mexico and Arizona where it is regarded as a cause of hayfever of secondary importance. Rydberg's cottonwood (*P. acuminata*) grows in situations similar to those of the valley cottonwood. At Deming and Silver City in New Mexico it is used as a shade tree along with the valley cottonwood, and in both states it is regarded as a minor cause of hayfever. Besides the native species, the European white poplar (*P. alba*) is occasionally cultivated and is reported as a possible cause of hayfever at Williams and Flagstaff in Arizona and at Gallup in New Mexico.

Ash.—Among the ashes the Arizona ash (*Fraxinus Toumeyii*) is the commonest, particularly in the irrigated valleys of Arizona where it is

believed to be of considerable importance in hayfever. The flowering ash (*F. cuspidata*) also occurs in the region and is reported from Gallup, New Mexico, as a possible cause of hayfever. It flowers somewhat later, generally in April.

Oaks.—More than twenty species of oak are recorded from the region, but for the most part they are not regarded as important in hayfever. A scrub oak (*Quercus turbinella* Greene) is believed to be of some importance in the mountainous parts of Arizona (PHILLIPS 1923), and other species, such as the bellota or black oak (*Q. Emoryi* Sarg.) and post oak (*Q. submollis* Rydb.) are regarded by WATSON and KIBLER (1922) as of slight importance.

Junipers.—The mountain cedar (*Juniperus mexicana*) in this region occurs only in part of Texas. In the region of Abilene it is said to be capable of causing hayfever from November to March (SELLERS 1934), though the bulk of its pollen is shed in December and January. Some half dozen other species occur in the region; among them the one-seeded juniper (*J. monosperma*) is recorded as very abundant in Seligman, Winslow, Williams and Flagstaff in Arizona, and Gallup in New Mexico, where it is believed to cause some hayfever. The alligator-bark juniper (*J. pachyphlaea*) also occurs abundantly almost throughout the entire region and is regarded as a possible cause of hayfever. These latter two species flower very early in spring but apparently not in midwinter as does the mountain cedar.

Mesquite.—*Prosopis juliflora* occurs principally in western Texas where it is said to be an important cause of hayfever (SELLERS 1929, 1934). It is also common in parts of southern New Mexico and Arizona.

The Grasses

Johnson Grass and Sorghums.—*Sorghum halepense* is abundant in many localities, particularly in western Texas, but is of only local importance in Arizona and New Mexico where it is said by PHILLIPS (1923) to affect only ranchers. Sorghum (*S. vulgare*) and its variety Sudan grass (*S. vulgare sudanense*) are cultivated, especially in western Texas where they may be minor contributors to hayfever.

The Grama Grasses.—Members of the genus *Bouteloua* are extremely common throughout the region. About ten species are counted, some of them constituting much of the original native range grass. The blue grama (*B. gracilis*), hairy or black grama (*B. hirsuta*), Rothrock's grama (*B. Rothrockii*) and six-weeks or needle grama (*B. aristoides* Griseb.) are regarded by WATSON and KIBLER (1922) as of secondary importance, and the tall or sideoats grama (*B. curtipendula*) and purple grama (*B. radicata* Griffiths) are reported as possible causes of hayfever in Arizona by LAMSON and WATRY (1933b), and blue grama, hairy grama and six-weeks or mat grama (*B. simplex* Lag.) are reported as possible causes of hayfever at Williams, Arizona, by LAMSON and WATRY (1934). They all flower in the late summer after the rains but do not shed enough pollen to be of any real importance in hayfever in spite of the great abundance in which they occur.

Finger Grass. — *Chloris virgata*, sometimes known as feather grass, a close relative of Bermuda grass, is regarded as of secondary importance in Arizona at higher elevations where Bermuda and Johnson grass do not grow. It flowers in late summer after the rains, but sheds so little pollen that it is relatively unimportant even though the plants may be numerous.

Salt Grass. — *Distichlis spicata*, since it is confined to the salt marshes and is a rather meagre pollen shedder, is of only local and minor importance. It is reported as a possible cause of hayfever at Winslow, Holbrook and elsewhere in Arizona.

Bluegrass or June Grass. — *Poa pratensis*, since it is extensively used for lawns wherever sufficient moisture can be maintained, may be an important cause of hayfever in some places. It is counted among the grasses of first importance in Tucson, Arizona (WATSON and KIBLER 1922), and its use as a lawn grass in Holbrook and Flagstaff, Arizona, is reported by LAMSON and WATRY (1933b, 1934).

Brome Grasses. — Members of the genus *Bromus* are particularly abundant in this region, the native perennial species forming a considerable portion of the forage in open woods of the mountain regions, but they all shed so little pollen that none is of much importance in hayfever. Downy-sheathed cheat or hairy chess (*B. commutatus* Schrad.), large mountain-brome (*B. marginatus*) and its variety the Great Basin brome (*B. polyanthus paniculatus* Shear), and downy brome (*B. tectorum*) are recorded in great abundance and as possible causes of hayfever at Williams in Arizona (LAMSON and WATRY 1934). It is difficult, however, to judge their importance, but it is likely that they are deserving of some consideration in hayfever studies.

Amaranths and Chenopods

Among the amaranths, the common pigweed is found in disturbed soils almost throughout the Southwest. The climate of this region is peculiarly favorable to its development, and as a result it appears to be more of a factor in hayfever than in most other regions. It is regarded by WATSON and KIBLER as of primary importance in Arizona, and is recorded by others in Phoenix, Flagstaff, Williams, Gallup and western Texas, where it is reported by SELLERS (1934) to be second in importance to careless weed (*A. Palmeri*). This latter species, though less widely distributed, appears to be much more important in regions where it does occur. It is stated by WATSON and KIBLER to be of primary importance in Arizona, and PHILLIPS reports that it is abundant throughout the Salt River valley in Arizona where besides being an invader of disturbed soils it is used in enormous quantity as a cover crop by citrus growers.

Spiny Amaranth and western water-hemp occur in this region only in western Texas where they are regarded as among the weeds of primary importance.

Tumbleweed (*Amaranthus graecizans* L.) is a common weed in this region sometimes regarded as a cause of hayfever but is probably of little or no importance.

Among the chenopods, lambsquarters occurs, as elsewhere, in consider-

able abundance in disturbed soils and must be regarded as a secondary contributing factor. It is recorded in varying degrees of importance in Tucson, Phoenix, Flagstaff and Williams in Arizona, Gallup in New Mexico, and in western Texas. A related species (*Chenopodium Watsoni* A. Nels.) common in Arizona and New Mexico, is recorded as a possible cause of hayfever at Williams in Arizona.

The saltbushes (*Atriplex*) are abundant throughout most of the Southwest. Wingscale (*A. canescens*), generally known as shadscale, is among the most important hayfever plants of the region. Annual saltbush (*A. Wrightii*) is less widely distributed but is counted among the most important hayfever plants in southern Arizona. Other species such as *A. lentiformis*, *A. polycarpa*, the true shadscale (*A. confertifolia*) and ribscale (*A. Powellii* S. Wats.) are mostly confined to the desert regions, particularly in Arizona where they undoubtedly cause some hayfever.

Russian Thistle. — *Salsola Pestifer* is by far the most important member of this group. It is now found in great abundance in many places in the Southwest, often outranking the ragweeds. It is among the worst hayfever plants of western Texas and in northern Arizona and New Mexico. It is creeping into southern Arizona. "After six years of adaptation it has finally gained a foothold in the valley and is now rapidly spreading but is not yet important" (PHILLIPS 1923).

Kochia. — Being closely related to Russian thistle the kochias are similar in appearance and habit and with pollen of similar allergenic properties. Two species are to be reckoned with; the burning bush or Mexican fire bush (*Kochia scoparia*) occurs at Seligman, Holbrook, Winslow and to a certain extent at Gallup, while the redsage (*K. americana*) is reported to be working into New Mexico. Neither species, however, is yet important in the Southwest.

The Ambrosieae

The ragweeds and their allies are represented by a large number of species but are much less important than in the East. The eastern short ragweed is occasionally found but hardly ever in considerable quantity. Its place is taken to a certain extent by western ragweed (*Ambrosia psilostachya*) which is abundant in southern Arizona, at Williams and at Flagstaff, but is in no way comparable with the short ragweed of the East. The eastern giant ragweed is not found in the region, but the western or Texas great ragweed (*A. aptera*) has a limited distribution in western Texas, parts of New Mexico and parts of Arizona, where it may occasionally be a severe local cause of hayfever.

False Ragweeds. — The members of the genus *Franseria* are of much greater importance than the true ragweeds. Bur ragweed (*F. acanthi-carpa*) occurs almost throughout the region while the slender ragweed (*F. tenuifolia*) is more abundant in the southern part of Arizona and New Mexico. These two are the most important of the late-flowering franserias. Low ragweed (*F. discolor*) is of only local distribution in the plains of Arizona and New Mexico. The early-flowering franserias are considered to be more serious causes of hayfever than the late-flowering species. Rab-

bit bush (*F. deltoidea*) is counted among the worst causes of early-summer hayfever but occurs only in Arizona, especially the southern part of the state. Canyon ragweed (*F. ambrosioides*) is limited to moist places in Arizona. Desert bursage or bush sandbur (*F. dumosa*) has only a limited distribution in desert plains of southwestern Arizona.

The Marshelders.— The genus *Iva* is represented by several species. Poverty weed (*I. axillaris*) is found, sometimes in great abundance, in alkaline soils almost throughout the region and is probably a local factor of secondary importance.

Prairie ragweed (*Cyclachaena xanthifolia*) grows along streams and in waste places in New Mexico and is a common weed in cultivated fields in some parts of the state. Elsewhere in the region it appears to be of no importance though it occurs to a certain extent. Coarse ragweed (*C. ambrosiaefolia* B. & H.) occurs in dry mesas and sand hills throughout the region.

Other members of the group which deserves attention are the greaseweed (*Hymenoclea salsola*), occurring only in the southwestern part of Arizona, Jecote (*H. monogyra*) occurring in desert regions throughout, and two species of *Dicoria*, *D. canescens* occurring in the sandy deserts of southern Arizona and *D. Brandegei* in sandy soil in valleys of Arizona and New Mexico. Both are mentioned by WATSON and KIBLER as possible causes of hayfever in Arizona.

Artemisias

Common Sagebrush.— *Artemisia tridentata* is abundant in the northern part of the region, and is regarded as a cause of hayfever only in parts of northern Arizona and New Mexico. Gray sage (*A. Wrightii*) and its close relative, *A. Carruthi* Wood, are common in the canyons and meadows of the Upper Sonoran zone of the mountains of northern New Mexico. Silvery wormwood (*A. filifolia*) occurs in the dry sandy plains and valleys of the Lower and Upper Sonoran zones almost throughout, and in the dry sandy valleys of New Mexico appears to occasionally cause a severe type of hayfever.

The Common Sunflower (*Helianthus annuus*), especially its variety, *lenticularis*, grows in enormous quantity throughout much of this region and is probably occasionally a local cause of hayfever.

REFERENCES

A number of excellent botanical studies have been made of the hayfever situation of the Southwest. The earliest of these was the memorable work of WATSON and KIBLER (1922), reporting from Tucson, Arizona, done in association with Professor J. J. THORNER of the University of Arizona. They find that the hayfever in Arizona lasts from about the end of January to the middle of November. They give a list of about a hundred plants capable of producing hayfever in the Southwest.

At about the same time as this pioneer work of WATSON and KIBLER was published, appeared the study of E. W. PHILLIPS (1922), reporting from Phoenix, Arizona. He states that hayfever in central Arizona lasts about nine months of the year, and that much of the pollen which causes it comes from the weed flora of the irrigated districts which are not intensively cultivated, and that: "As population and irrigation increase so does the amount of pollen in the air and the number of those made ill by it". He reports the principal causes to be cottonwoods, principally Arizona cottonwood,

Arizona ash, Bermuda grass, sorghum and several species of *Atriplex*, careless weed, pigweed, bur ragweed (*Franseria acanthicarpa*), rabbit bush and species of *Artemisia*.

In a second paper PHILLIPS (1923) states that about 10 per cent of the population in central Arizona have hayfever, but no Indians and no Mexicans were found to be affected by it. Hayfever in the irrigated valleys is caused principally by Bermuda grass, to a lesser extent by Arizona cottonwood, Arizona ash, Johnson grass, carelessweed, wingscale and, to a slight extent, by rabbit bush. In the hill and mountain country hayfever is generally due to species of junipers, causing mild symptoms in late winter and early spring, scrub oak and cottonwoods producing only minor effects, Russian thistle and wingscale which are the most important, and, in restricted areas of the northern part, bur ragweed and sagebrush, slender ragweed in the southern part, and in scattered localities western ragweed, field sagewort and gray sage.

In a later paper PHILLIPS (1928) draws attention to the absence of eastern short ragweed but says that: "Persons who are primarily sensitized to the eastern ragweed always react more or less to the false ragweeds, western ragweed and rabbit bush, the strength of their reactions being usually in the order named". As a result of this cross sensitization, eastern ragweed cases usually have hayfever the first year of their arrival in Arizona. Such, however, is not true of eastern grass cases; in Arizona they are nearly always free from hayfever for three to five years before they succumb to the effects of Bermuda grass pollen.

PHILLIPS also draws attention to the changing character of the flora of Arizona. In speaking of slender ragweed (*Franseria tenuifolia*) he says: "This plant, always present in the Salt River Valley in scattered patches, has hitherto done no damage, so far as I know. But conditions are changing; because of the city's rapid growth, considerable land that was formerly under clean cultivation has been taken over by real-estate developments and lies fallow. The false ragweed has moved onto the vacant lots. Last fall, stimulated by early rain, it pollinated freely enough to affect those sensitized to the ragweed group . . . The same is true of carelessweed". In a later note PHILLIPS (1930) states: "The area infested by this plant [slender ragweed] was much greater than in former years. There were found at the edges of the city, whole fields of it. Patches occurred along the roadsides, much as the true ragweed grows in the East". Russian thistle and western ragweed to a lesser extent at this time were observed to be invading the Salt River Valley.

In a still later paper PHILLIPS (1932) summarizes his earlier work. He emphasizes the fact that there are two ragweed seasons in Arizona. The first which lasts about a month, from March 10 until the hot weather sets in, is due to *Franseria dumosa*, *F. deltoidea* and *F. ambrosioides* and, in the southwestern part of the state, to *Hymenoclea Salsola*. The second ragweed season, milder than the first, begins about the middle of September and lasts about six weeks, and is due to *Franseria tenuifolia*. The worst of all hayfever plants, he finds to be Bermuda grass, which, he says, "Makes more trouble than all the rest combined". It is still possible, however, to escape hayfever in Arizona for "No one, whether from within or without the state, has pollen symptoms at the resorts located in the pines and remote from cultivation".

WILSON (1934) reporting from Tucson, Arizona, on problems of hayfever of the Southwest, states that hayfever is particularly bad in the region not only because of the great abundance of atmospheric pollen, but also because of the drying effect that the desert atmosphere has on the mucous membranes, rendering them more than usually susceptible to the effects of pollen. In discussing WILSON's paper both WATSON and KIBLER noted the spread of Russian thistle into Arizona within the past 12 years in sufficient quantity to become a real menace to hayfever sufferers.

A valuable series of surveys of hayfever plants of the Southwest has been conducted by LAMSON in collaboration with ALVA WATRY. These papers are notable for their high botanical quality, and very excellent photographs of hayfever plants, taken both in the field and in the studio. The first of this series, A Botanical Survey of Needles, California (WATRY and LAMSON 1931) is considered in connection with our discussion of the hayfever plants of southern California (p. 197) so need not be discussed here though the material applies to this region to a certain extent because Needles is on the boundary between California and Arizona. Their second study deals with the anemophilous plants of Seligman, in central Arizona near Prescott. The authors fur-

nish a list, with their times of flowering and relative abundance, of about 40 plants with hayfever possibilities.

Another study by these authors (LAMSON and WATRY 1933a) deals with the hayfever plants of Winslow and Holbrook in the valley of the Little Colorado River in northern Arizona. The authors furnish pollen calendars of the anemophilous plants with hayfever possibilities. Hayfever there they find, is mainly caused by the pollen of grasses and chenopods, though Bermuda grass is nearly absent.

LAMSON and WATRY (1934) in Survey of a Botanic Oasis in the Desert of Northern Arizona, discuss the hayfever plants of the San Franciscan Volcanic Field, at an elevation of 6500 to 7000 feet, including the towns of Flagstaff and Williams. They emphasize the localized distribution of the various species. For the most part hayfever plants are lacking, since the natural vegetation is of the montane forest type. The most important intruder appears to be Russian thistle.

WATRY and LAMSON (1934) report a study of the hayfever situation at Gallup in the northwestern corner of New Mexico. The town is at an altitude of 6500 feet. The most abundant hayfever plants are Russian thistle, wingscale and sagebrush. Many grasses are abundant but these are mostly native species growing naturally so are unimportant, and Bermuda grass is absent.

The problem of hayfever in western Texas has been extensively studied by SELLERS, reporting from Abilene. This author, as already noted (p. 114) has repeatedly emphasized the importance of mesquite in hayfever, and its abundance throughout a large part of Texas. SELLERS and ADAMSON (1932) find that the most important hayfever plants in this region are members of the *Chenopodiaceae* and *Amaranthaceae*, more important than the ragweeds. SELLERS (1934, 1935) reports that in the west Texas area the grasses and *Chenopodiales* are the most important causes of spring and early-summer hayfever.

VII. Southern California:—

Artemisia. — HALL (SCHEPPEGRELL 1917a) states: "In California *Artemisia heterophylla* and *A. tridentata* are the principal hayfever plants". It should, however, be pointed out that the latter species, though probably the most important hayfever plant of the Great Basin area, is in southern California represented in quantity only on the desert slopes of the mountains; west of the mountains where the country is most thickly populated it is scarcely known. *A. heterophylla*, on the other hand, grows almost throughout the region, scattered or in masses, often forming thickets on river banks or along ditches especially in low moist land. Also among species of first importance are *A. californica* and *A. dracunculoides*. The former is particularly abundant all along the coastal slope where it often forms dense masses, and the latter is abundant in the San Jacinto and San Bernardino Mountains, and locally at Los Angeles, but for the most part is not abundant enough in southern California to be of much importance in hayfever.

Atriplex. — The saltbushes in southern California are of relatively little importance west of the mountains. Wingscale, bractscale and lenscale occur abundantly in the Colorado desert and alkali interior where they are among the most important causes of hayfever. *A. canescens*, however, also occurs occasionally on the coastal slope in Ventura and San Diego Counties.

Ambrosia pumila. — The dwarf or Tia Juana ragweed "Inhabits Lower California and reaches its northern limit in southwestern San Diego County, California, where it may be a local factor" (ABRAMS 1932).

Franseria. — Of the false ragweeds HALL (SCHEPPEGRELL 1917a) points out that bur ragweed is abundant in the southern and eastern part of the

state, especially in sandy plains and fields. Slender ragweed also occurs in similar places but is much less common. The desert bur sage (*F. dumosa*) is found only in the hot dry deserts east of the mountains but in these regions it grows in great abundance.

Table VII, HAYFEVER PLANTS OF SOUTHERN CALIFORNIA : —

SPECIES	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
<i>Juglans californica</i> (Calif. bl. walnut)...												
<i>Quercus agrifolia</i> (Coast live oak).....												
<i>Platanus orientalis</i> (Oriental plane tree)												
<i>Platanus racemosa</i> (West. sycamore)...												
<i>Populus Fremontii</i> (Calif. cottonwood)...												
<i>Cynodon Dactylon</i> (Bermuda grass).....												
<i>Lolium perenne</i> (Ryegrass)												
<i>Phalaris minor</i> (Canary grass)												
<i>Avena fatua</i> (Wild oat)												
<i>Avena barbata</i> (Wild oat)												
<i>Lolium temulentum</i> (Darnel)												
<i>Poa pratensis</i> (Kentucky bluegrass)....												
<i>Sorghum halepense</i> (Johnson grass).....												
<i>Dactylis glomerata</i> (Orchard grass)....												
<i>Distichlis spicata</i> (Salt grass).....												
<i>Bromus carinatus</i> (Bromegrass)												
<i>Bromus rigidus</i> (Rippugrass)												
<i>Plantago lanceolata</i> (English plantain)..												
<i>Amaranthus graecizans</i> (Tumbleweed)...												
<i>Amaranthus retroflexus</i> (Pigweed).....												
<i>Atriplex canescens</i> * (Wingscale)												
<i>Atriplex bracteosa</i> * (Bractscale)												
<i>Atriplex rosea</i> (Redscale)												
<i>Atriplex argentea</i> (Silverscale)												
<i>Atriplex polycarpa</i> (Allscale)												
<i>Atriplex lentiformis</i> * (Lenscale)												
<i>Chenopodium album</i> (Lambsquarters)...												
<i>Salsola Pestifer</i> (Russian thistle).....												
<i>Artemisia dracunculoides</i> * (Dragon sage)												
<i>Artemisia heterophylla</i> * (Calif. mugwort)												
<i>Artemisia californica</i> (Coast sagebrush)												
<i>Artemisia biennis</i> (Biennial wormwood)												
<i>Artemisia tridentata</i> * (Sagebrush).....												
<i>Ambrosia psilostachya</i> (West. ragweed)												
<i>Ambrosia pumila</i> * (Dwarf ragweed)....												
<i>Franseria acanthicarpa</i> (Bur ragweed)...												
<i>Franseria tenuifolia</i> (Slender ragweed)...												
<i>Franseria dumosa</i> * (Desert bur sage)...												
<i>Hymenoclea Salsola</i> * (Greasebush).....												
<i>Iva axillaris</i> (Poverty weed).....												
<i>Xanthium pennsylvanicum</i> (Cocklebur)												
<i>Xanthium spinosum</i> (Spiny clotbur)....												

* Discussed in the accompanying paragraphs.

Hymenoclea Salsola. — Greasebush or Romerillo is chiefly of the deserts where it is common on low hills and is regarded as among the most important hayfever plants (ABRAMS 1932). On the coastal slope it occurs only in northern Santa Barbara County and is probably of little or no importance.

REFERENCES

The hayfever plants of southern California are exceptionally well known and their importance in hayfever understood largely because some of the world's leading botanists

happened to live in California and gave their whole-hearted coöperation with the local allergists in their hayfever studies. From coöperation of this kind arose the notable work "Hayfever Plants of California" (HALL 1922) in which all the species known to cause hayfever, and those with hayfever possibilities, throughout the state are listed with their times of flowering, their abundance and distribution within the state, together with records of allergic reactions obtained with their pollen in the clinics of Drs. CHAMBERLAIN, PINESS, ROWE, SCHEPPEGRELL, SELFRIDGE, and WATSON. This work published by HALL forms the botanical foundation upon which most of the later investigations have been based. HALL (SELFIDGE 1918) also reports a survey of California and Nevada, and, associated with Dr. SCHEPPEGRELL (SCHEPPEGRELL 1917a), contributes a comprehensive study of the rôle of the artemisias, marshelders, false ragweeds and cockleburrs of this region. To the same author (HALL 1917) we are also indebted for a study of the relation of farm weeds of the region to hayfever, and for the first definite proof (HALL 1918) that California black walnut pollen is a serious cause of hayfever throughout much of southern California.

A notable contribution of similar kind is "The Hayfever Plants of the Western States" (ABRAMS 1932). This study covers the area from California east to Texas and north to Oregon, but Part I, all that is so far published, treats only members of the *Ambrosiaceae*. PINESS, MILLER and McMINN (1926) in their botanical survey of southern California give a list with pollinating dates, of all the known hayfever plants and those with hayfever possibilities. The very valuable table from this work has been reprinted by VAUGHAN (1931). PINESS (1925), PINESS and McMINN (1927) furnish a comprehensive study of the pollens of the most important hayfever plants of California, illustrated by photomicrographs and drawings of the pollen grains, and with a key for their identification.

Intensive local studies of several regions have also been made. PINESS and MILLER (1930) made detailed studies of two isolated communities, one a mining community the other a potash community, both in desert conditions and with an unusually high pollen incidence. They found that the great majority of people in these communities began to have hayfever only after one to four years residence there. In the mining community the principal causes of hayfever were found to be Bermuda grass, Russian thistle, wingscale and redscale, while in the potash community the principal cause was Bermuda grass. He says that the high general incidence of hayfever in these communities, taken in consideration with the low general incidence of positive heredity among the inhabitants, suggests the possibility that even so-called nonallergic individuals may become sensitized by a super-abundance of pollen.

WATRY and LAMSON (1931) in "A Botanical Survey of Needles, California" point out that in and about Needles, since it is situated on the Colorado River, the vegetation departs widely in character from that of the surrounding desert. The real causes of hayfever in Needles are found to be Bermuda grass, growing between the dyke and the river and in lawns, and the three species of saltbush, *Atriplex lentiformis*, *A. polycarpa* and *A. elegans*. Other plants of the region of less but still considerable importance, are willow (*Salix nigra*) and poplar (*Populus Fremontii*) flowering in February, and the desert bur-sage (*Franseria dumosa*), and *Hymenoclea Salsola* later in the season. But there is, at present, no Russian thistle nor wingscale.

STEALY (1936) contributes a two-and-a-half year study of the pollen situation in San Diego, giving records of atmospheric pollen together with their relation to wind velocity and rain fall. He finds that pollen allergy at San Diego is a perennial disorder, but the amount of pollen varies from year to year depending principally upon rain fall. The principal sources of pollen he finds to be the ragweeds, false ragweeds, chenopods, amaranths and grasses.

VIII. The North Pacific States (Northern California, Nevada, Oregon, Washington) : —

Acacia. — Many Australian species of acacia have been introduced into this region and are extensively used as shade trees in streets and parks in the towns and cities of California; they are especially abundant in San

Table VIII, HAYFEVER PLANTS OF THE NORTH PACIFIC STATES : —
(Northern California, Nevada, Oregon, Washington)

SPECIES	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Acacia* (Acacia)	I											
Acer Negundo (Boxelder)												
Acer* (Maples)												
Alnus* (Alders)	I											
Betula* (Birches)												
Corylus californica (California hazel)...												
Juglans californica* (Calif. bl. walnut)												
Platanus acerifolia (London planetree).												
Populus* (Cottonwoods)		I										
Salix sitchensis (Sitka willow)												
Salix* (Willows)												
Quercus Douglasii (Blue oak)												
Quercus agrifolia (Coast liveoak).....												
Quercus Wislizenii (Interior liveoak)...												
Quercus* (Oaks)												
Eucalyptus* (Gumtrees)												
Olea europaea (Olive).....												
Ligustrum (Privets)												
Fraxinus* (Ashes)												
Chamaecyparis Lawsoniana* (Cypress)..												
Schinus molle (Pepper tree).....												
Garrya elliptica* (Silk-tassel bush)....	I											
Morus (Mulberry)												
Agrostis alba (Redtop)												
Avena fatua (Wild oat).....		I										
Avena barbata (Wild oat)												
Bromus carinatus (California brome)...												
Bromus hordeaceus (Soft cheat).....												
Bromus rigidus (Ripgut grass).....												
Bromus (Brome grasses)												
Cynodon Dactylon (Bermuda grass)....												
Dactylis glomerata (Orchard grass)....												
Distichlis spicata (Saltgrass)												
Hordeum murinum (Mouse barley).....												
Lolium perenne (Perennial ryegrass)...												
Lolium temulentum (Darnel)												
Lolium multiflorum (Italian ryegrass)...												
Holcus lanatus (Velvet grass).....												
Phalaris californica (Canary grass)....												
Poa annua (Low spear-grass).....												
Poa compressa (Canada bluegrass)....												
Poa pratensis (June grass).....												
Ammophila arenaria (Beach grass).....												
Sorghum halepense (Johnsongrass).....												
Festuca (Fescue grasses)			I									
Anthoxanth. odorat. (Sw. vernalgrass)..												
Phleum pratense (Timothy)												
Koeleria cristata (Western June grass)...												
Agropyron Smithii (Bluestem)												
Agropyron repens (Quack grass)												
Amaranthus retroflexus (Pigweed).....												
Amaranthus graecizans (Tumbleweed)												
Atriplex rosea (Red orach)												
Atriplex canescens* (Wingscale).....												
Atriplex* (Saltbushes)												
Chenopodium album (Lambsquarters) ..												
Chenopodium ambrosioides (Mex. tea)...												
Salicornia ambigua* (Pickleweed).....												
Salsola Pestifer* (Russian thistle).....												
Plantago lanceolata (English plantain).												

* Discussed in the accompanying paragraphs.

Table VIII. — Concluded: —

SPECIES	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
<i>Rumex Acetosella</i> (Sorrel dock).....			I									
<i>Rumex*</i> (Docks)												
<i>Amb. psilostachya</i> (West. ragweed)....												
<i>Franseria bipinnatifida*</i> (Beach sandbur)												
<i>Franseria Chamissonis*</i> (False ragweed)												
<i>Franseria acanthicarpa*</i> (Bur ragweed)...												
<i>Franseria tenuifolia*</i> (Slender ragweed)...												
<i>Iva axillaris</i> (Poverty weed)												
<i>Cyclachaena xanthifolia*</i> (Burweed)....												
<i>Xanthium spinosum</i> (Spiny clotbur)....												
<i>Xanthium</i> (Cocklebur)												
<i>Artemisia californica</i> (Coast sagebrush)												
<i>Artemisia heterophylla</i> (Mugwort).....												
<i>Artemisia tridentata*</i> (Sagebrush)												
<i>Artemisia spinescens*</i> (Budbrush).....												
<i>Artemisia dracunculoides</i> (Dragon sage)												
<i>Artemisia biennis</i> (Biennial wormwood)												
<i>Artemisia ludoviciana</i> (Prairie sage)...												
<i>Helianthus annuus*</i> (Sunflower).....												
<i>Taraxacum officinale</i> (Dandelion)												

* Discussed in the accompanying paragraphs.

Francisco. Though insect pollinated, it is suspected that their pollen is capable of causing hayfever. In hayfever studies the different species are rarely differentiated. ROWE (1932), however, mentions *Acacia melano-carpa* as a common species in San Joaquin County, California. Native species do not occur.

Maples. — Besides boxelder, which is widely distributed in this region along stream bottoms and occasionally planted as a shade tree, the silver maple (*Acer saccharinum*) and sugar maple (*A. saccharum*) are planted in city streets. Oregon or Big-leaf maple occurs rather abundantly in the valleys and protected coast region of northern California (ROWE and HOWE 1935) and northward. But no maple appears to be of importance in hayfever.

Alders. — Besides the white alder (*Alnus rhombifolia*), which is perhaps the commonest in California, red alder (*A. rubra*) is recorded for California, and thin-leaved alder (*A. tenuifolia*) and Oregon alder (*A. oregona*) are recorded for western Oregon and Washington.

Birches. — White birch, both in its natural form (*Betula alba*) and the weeping form (*B. alba laciniata pendula*) are planted in city streets and parks. In eastern Oregon and Washington the spring birch (*B. fontinalis*) is reported to be the common species.

Walnuts. — Besides the native species, *Juglans californica* and *J. Hindsii* which are known to be important causes of hayfever in California, the eastern black walnut (*J. nigra*) and the English walnut (*J. regia*) are extensively planted and are regarded by ROWE (1928, 1929, 1932) as contributory causes of hayfever.

Cottonwoods.— Several species of *Populus* are common in the region. In California *P. deltoides* and *P. Fremontii* are regarded as probable causes of hayfever. These and other species flower in California mostly in March and early April. In Oregon and Washington *P. tremuloides* and *P. trichocarpa* are recorded as causes of hayfever in April and May.

Willows.— Many species of *Salix* occur in the region; the arroyo willow (*S. lasiolepis*), sitka willow (*S. sitchensis*), red willow (*S. laevigata*) and dune willow (*S. Piperia*) are recorded as possible causes of hayfever in various parts of the region, but none is believed to be important.

Oaks.— *Quercus* is represented by many species. The coast live oak (*Q. agrifolia*), interior live oak (*Q. Wislizenii*), valley oak (*Q. lobata* Née), scrub oak (*Q. dumosa*), blue oak (*Q. Douglasii* Hook. & Arn.) and others are common in California, while Oregon oak (*Q. Garryana*) and California black oak (*Q. Kelloggii* Newb.) are common in Washington and Oregon.

Eucalyptus.— Several species of gum tree are extensively cultivated in California. Though the trees are primarily insect pollinated, the pollen has been recorded in the air by DEAMER and McMINN (1935).

Ash.— Oregon ash (*Fraxinus oregona*) is common throughout much of the region, and the European flowering ash (*F. Ornus*) and Arizona ash (*F. velutina*) are planted as street and roadside trees, flowering in February and March in California and about April in Washington and Oregon.

Elms.— Though no elms occur naturally on the Pacific coast, ROWE (1932) records the European elm (*Ulmus procera*), in several varieties, and other species planted along streets and in parks in central California.

Lawson Cypress.— *Chamaecyparis Lawsoniana* occurs naturally throughout much of the region and it and the related cypresses (*Cupressus*) and junipers are planted as street and park trees.

Saltbushes.— Many species of *Atriplex* occur in the region. Perhaps the most abundant is *A. patula*, including its variety *hastata*. This is regarded by ROWE (1928) as among the most important plants of the San Francisco Bay region, based upon the skin reactions obtained with its pollen. It is, however, restricted to the salt marshes, principally along the coast. Red orache is counted by ROWE (1932) among the most important plants of San Joaquin County, California. *A. coronata*, *A. leucophylla*, *A. semibaccata* and other species are probably of some importance in California. *A. canescens* is recorded among the most important hayfever plants of Nevada (ALBERT and DEBELL 1927) but not elsewhere in the region.

Pickleweed.— *Salicornia ambigua* occurs only in salt marshes principally along the coast.

Russian Thistle.— *Salsola Pestifer* is extremely abundant east of the mountains. It is regarded as the most important hayfever plant of Nevada (ALBERT and DEBELL 1927) and is also of the utmost importance in eastern California, Oregon and Washington, and is regarded by ROWE (1932) as among the most important plants of San Joaquin County, California, growing on "alkaline sand, roadsides and grain fields", but it does not occur to any extent elsewhere along the coast.

Docks. — Besides the sorrel dock which occurs throughout the region, curly dock (*Rumex crispus*) is likewise widely distributed. Western dock (*R. occidentalis*), green dock (*R. conglomeratus*) and fiddle dock (*R. pulcher*) are abundant in California (ROWE and HOWE 1935).

Western Ragweed. — *Ambrosia psilostachya* is important throughout most of the region but is absent from western Oregon and western Washington.

False Ragweeds. — *Franseria bipinnatifida* and *F. Chamissonis* occur principally along the sea shore, while *F. tenuifolia* and *F. acanthicarpa* occur in the eastern part of the region.

Marshelders. — *Iva axillaris* and *Cyclachaena xanthifolia* are important only in the eastern part of the region.

Sagebrushes and Mugworts. — *Artemisia pycnocephala* occurs only on the sand dunes of the sea shore. Common sagebrush is among the most important hayfever plants in the eastern part of the region, especially eastern Oregon and eastern Washington, but does not occur to any extent west of the mountains. Budbrush (*A. spinescens*) is especially common in Nevada where it appears to be of some importance in hayfever.

Sunflower. — *Helianthus annuus*, both wild and cultivated, is extremely abundant throughout much of the region. ROWE (1932) reports 1000 acres in San Joaquin County, California, devoted to its culture. Though insect pollinated it is probably a local factor of some importance.

Pepper Tree. — *Schinus Molle* L. is cultivated in parts of California and is suspected of being a local cause of hayfever. Of it SCHEPPEGRELL (1925) states that it is reported by Professor GEORGE POTTS of the Department of Botany, Greys University College, Bloemfontein, South Africa, to be a severe cause of hayfever in Bloemfontein, Kimberley and other towns of South Africa where it is extensively cultivated. This was proved by catching the pollen on atmospheric pollen plates when the trees were flowering, and by cutaneous tests with the pollen on patients afflicted with hayfever at the same time. The tree is native of tropical America and belongs to the *Anacardiaceae* or Sumac family.

REFERENCES

The earliest published contribution to our knowledge of the hayfever situation in this region, as far as I know, is that of SCHEPPEGRELL (1917a), done in association with Professor H. M. HALL. Though this paper is now twenty-seven years old it is still of great value for its excellent descriptions and illustrations of hayfever plants, and accurate estimates of the importance of their pollen in hayfever.

SELFRIDGE (1918) published in his paper on hayfever in California an excellent botanical survey of California and Nevada by H. M. HALL, in which all the plants known to cause hayfever and those with hayfever possibilities are listed in their biological classification. SELFRIDGE (1919) listed fifteen species of hayfever plants with which he considered it necessary to test hayfever patients for pollen sensitization in San Francisco, recording the number of reactions he got from the pollen of each with a selected group of cases. Broncho grass and wild oat head the list, with salt grass, canary grass, June grass and wheat not far behind. Plantain, mugworts, poverty weed and sagebrush also gave a fair proportion of reactions. The spring type of hayfever, due to grasses, he found to predominate in this part of California. The same author (SELFRIDGE 1920) extended his list of necessary pollens to include southern California,

taking care to emphasize the necessity of using only those of such species as are found locally and the futility of employing those of related species from the East, the only ones which the eastern commercial firms were able to supply at that time. Of some interest is his record of "My discovery that the pollen of ray grass (*Lolium perenne*) is perhaps the most important hayfever producer of all the grass family found on the Pacific Coast". This grass had been omitted from his earlier list even though its primary importance in California, Washington and Oregon had already been pointed out by SCHEPPEGRELL (1917a).

HALL (1922) summarized and extended his work already done in association with SCHEPPEGRELL and SELFRIDGE in his catalogue of hayfever plants of California. This work includes 175 species of plants with proved or possible hayfever potentialities and 15 others which he points out are frequently but erroneously regarded as causes of hayfever. The relative importance of each of the others is indicated; "determined by field observations as to the abundance of the plants, by the amount and size of the pollen produced, and by reports as to the frequency and extent to which positive results have been obtained with the extracts". In determining the first two of these criteria HALL drew upon his extraordinary powers of observation and his superb knowledge of Western botany; in the third criterion he had the able assistance of such outstanding allergists as CHAMBERLAIN, PINESS, ROWE, SCHEPPEGRELL, SELFRIDGE and WATSON. The result of this has been that the catalogue stands as valuable today as a general survey of California as when it was written, for so complete and meticulously accurate was HALL's work that little can ever be added to it or taken from it, except as the flora changes through the destructive activities of human incursions. But, as HALL points out, "hayfever of this region is very much a local problem; a species of first rank in one district may be of minor significance in another, and vice versa". To offset this to a certain extent he furnished supplementary district lists for the San Francisco Bay Communities, Sacramento and San Joaquin Valleys, and Los Angeles-Pasadena district. The road to further development of our knowledge of the hayfever botany of this region from this time on has lain almost entirely in the study of the hayfever conditions of more and smaller districts.

A series of such studies was instituted by ROWE (1928). In his first paper he records the result of a botanical survey and atmospheric pollen counts of the east shore of San Francisco Bay. The botanical survey presents a list of all the plants known to cause hayfever and those with hayfever possibilities, together with their relative abundance in the various communities of the district, and their times of flowering. The atmospheric pollen records show that pollen is found in the air throughout the year, the least occurring in August and September.

ROWE (1929) furnishes a botanical survey of San Francisco, giving a list of all the plants of the district known to cause hayfever or with hayfever possibilities, showing their flowering periods and relative abundance in the different parts of the district. He points out that certain differences exist between this district and that of the east shore of San Francisco Bay. *Bromus maritimus*, *Franseria Chamissonis*, and *Artemisia pycnocephala* are common enough to be taken into definite account in treating patients who live in San Francisco, while these plants are absent from the east shore of San Francisco Bay. Golden Gate Park with its large numbers of such trees as acacia, oak, birch, sycamore and an abundance of grasses, is a source of much pollen which is carried to the residential districts of the city.

ROWE (1932) presents a botanical survey of San Joaquin County in central California, conducted by Professor E. E. STANFORD. A list is furnished including "that portion of its flora which produces or may possibly produce pollen sensitization," and giving the relative importance, abundance, dates of flowering and distribution within the district of the various species. He finds marked differences between the flora of this district and those of the two previous reports. The San Joaquin area, especially the irrigated section is characterized by an abundance of *Amaranthaceae* and *Chenopodiaceae*, including such notable hayfever plants as Russian thistle and species of *Atriplex*. These floristic differences he finds to be decidedly reflected in the character of the hayfever most frequently encountered: "Patients from San Joaquin County usually give large reactions to amaranth, chenopod, *Atriplex* and *Salsola kali* [Russian

thistle] pollens, whereas reactions to the *Artemisia* pollens, with or without reactions to the foregoing chenopod pollens are the rule in patients living in the Bay counties".

Rowe and Howe (1935) report a botanical survey of northwestern California, dealing with the regions west of the Klamath Mountains, including the counties Del Norte, Humboldt, Trinity, Mendocino, Lake and Sonoma. A list is furnished of anemophilous plants with their dates of flowering and relative abundance. The grasses produce most of their pollen in late spring (May) and through the summer to the end of July. Along the coast in the north the silk-tassel bush (*Garrya elliptica* Dougl.) is commonly found. The most important regions from the view-point of the number of hayfever-producing plants are the Humboldt Bay littoral, the Russian River Valley and the plains about Clear Lake.

DEAMER, JENKINS and LAZARUS (1938) report a pollen survey on the Arcata district, Humboldt County. They find the pollinating season for grasses unusually long, extending from April to November, and the pollen of ragweed more abundant than in the San Francisco area. On their slides they encountered the pollens of grasses, ragweed, sagebrush, amaranth, chenopod, plantain, dock, nettle, alder, cypress, pine, cottonwood, willow, elm.

The botanical aspect of the hayfever situation in Oregon has been studied by CHAMBERLAIN (1927), listing the most important plants with the dates of their pollination. The state is divided from north to south by the Cascade mountains. East of the mountains is an elevated plateau with a relatively dry climate and much wind, conducive to anemophilous pollination. Most of the hayfever of this region is caused by grasses, species of *Atriplex*, Russian thistle and the artemisias. The western part of the state comprises several river valleys presenting various types of flora. The largest of these is the Willamette valley in which is located the city of Portland. The author finds that: "Approximately 95 per cent of all hayfever in Oregon is of the early or mid-summer type, caused by the pollens of the grasses". Forty-five per cent of the cases in one group were found to be sensitive to the pollens of trees and 60 per cent to the pollen of late-flowering weeds.

STIER, HOLLISTER and BONSER (1930) report a botanical survey of the hayfever-producing plants of Oregon and Washington. This report also includes the states, Idaho, Montana, Wyoming, Utah and Colorado, is referred to again in the discussion of these states. The authors furnish a list of anemophilous plants, and others, with hayfever possibilities, giving their relative abundance in the eastern and western parts of Oregon and Washington, and the life zones or elevations at which they are characteristically found. Russian thistle is found to occur principally east of the mountains.

The hayfever flora of western Oregon and Washington these authors report to be quite different. The most important factor appears to be velvet grass. Timothy, orchard grass, ray grass, Italian rye grass, Kentucky blue grass, brome grasses, and plantain are also common and important contributors to hayfever during early summer. The authors also find that the common dandelion grows in enormous abundance and to unusual size and believe it to be an important factor in hayfever, even though it is insect pollinated.

SCHONWALD (1937) presents a pollen calendar for western Washington, and curves for the atmospheric pollen of the principal species. In the vicinity of Seattle he finds no ragweed, artemisia or Russian thistle. The principal causes of hayfever he finds to be hazel, alder, birch, poplar, maple and elm among the trees, and June grass, orchard grass, ray grass, velvet grass and plantain among the grasses and weeds. This author also finds that the common bracken fern (*Pteris aquilina* L.) is exceedingly common, and its spores are caught in large numbers on his pollen slides from July to September. Also many hayfever patients exhibit sensitivity to bracken spores and respond favorably to treatment with their extract.

STROM (1940) has recently furnished a pollen survey of Seattle and vicinity. He finds that tree hayfever occurs from February 1 to March 15 and is mostly due to the pollen of alder and birches which latter flower in April. Grass hayfever he finds to occur from April to mid June. Weed hayfever which occurs in the latter part of the summer, he finds to be of little importance, caused mainly by the pollen of goosefoot,

pigweed and mugworts. He reports that, though ferns are common in the region, they cause no symptoms of hayfever.

Of special interest in this connection is the work of PIEMEISEL and LAWSON (1937) on the types of vegetation in the San Joaquin valley. This study was made to determine the effect of the surrounding vegetation on the curly-top disease affecting such plants as beets, tomatoes, melons, squash and other important crop and ornamental plants. The authors furnish detailed maps showing the distribution of the various types of vegetation, both before its occupation by white settlers and in its present condition. "The San Joaquin Valley", they say "is a meeting place of the desert formations of the interior, the Mohave and Colorado deserts, and the grassland and broad sclerophyll formations of the Pacific slope". The plant formations as originally occurring were tree savanna, consisting of a scattered growth of oak trees and an undergrowth of perennial grasses, Pacific grassland, originally consisting of grasses 'as the native perennial bunchgrasses and the relatively harmless native plains grasses, desert saltbrush formation, consisting chiefly of *Atriplex polycarpa* and other species of *Atriplex*, and the lowland types of vegetation, consisting principally of such plants as seepweed (*Dondia Moquini*), alkali heath and salt grass, and in the wetter situations, pickleweed. But owing to improper agricultural use of much of the land the original flora has given way to native and introduced weeds which serve as intermediate hosts for the insect vectors of the plant virus diseases. Among these are included such notable causes of hayfever as Russian thistle, wild oat, red brome, slender fescue, mouse barley, Australian saltbush, bract scale and fogweed. The authors close their discussion with these words: "The correction of two uneconomical practices, intermittent farming and destructive grazing, is in accordance with the general principles of land conservation. Such a correction would also result in greatly reducing the leaf hopper population and the curly top damage to the crops". And to this one may also add, much of the late-summer type of hayfever.

IX. The Rocky Mountain States (Idaho, Montana, Wyoming, Utah, Colorado): —

In the main the hayfever of the region falls into three seasons as in the East. The first, of relatively slight importance, lasts from March to May, and is due principally to the cottonwoods or poplars, boxelder and birch. The second season, accounting for possibly one third of the cases, begins early in May and continues into July, and is due to the grasses, principally the introduced agricultural species such as timothy, redtop, orchard grass, June grass, the fescues and wheat grasses. Bermuda grass is not a factor, though it has been reported to occur in some parts of this region. The third season accounting for about 75 per cent of the hayfever, begins about July the first and continues until October, and is due to Russian thistle, sagebrush and other artemisias, amaranths and chenopods, with the ragweeds, false ragweeds and prairie ragweed playing a minor rôle, and this only locally. The short and tall ragweeds are abundant enough to be important in the extreme eastern part of the region and the short in part of Utah, but elsewhere neither they nor other members of the ragweed tribe are important causes of hayfever.

Trees

Junipers. — *Juniperus utahensis* occurs in the Upper Sonoran zone throughout much of the region flowering in April (TEMPLETON 1924). *J. monosperma* and *J. scopulorum* are recorded from the region of Pikes Peak and Colorado Springs (SERVICE 1934).

Poplars and Cottonwoods.— Western or river cottonwood (*Populus Sargentii*), willow-leaf cottonwood (*P. angustifolia*), Rydberg's cottonwood (*P. acuminata*) and the trembling aspen (*P. tremuloides*) are the

Table IX, HAYFEVER PLANTS OF THE ROCKY MOUNTAIN STATES:—
(Idaho, Montana, Wyoming, Utah, Colorado)

SPECIES	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
<i>Juniperus*</i> (Junipers)												
<i>Betula fontinalis</i> (Mountain birch).....												
<i>Alnus tenuifolia</i> (River alder)												
Populus Sargentii (Western cottonwood)												
<i>Populus*</i> (Cottonwoods)												
<i>Salix</i> (Willows)												
Acer Negundo* (Boxelder)												
<i>Acer*</i> (Maples)												
<i>Quercus Gambellii</i> (Scrub oak).....												
<i>Quercus Gunnisonii</i> (Scrub oak)												
<i>Taraxacum officinale</i> (Dandelion)												
Phleum pratense (Timothy).....												
Agrostis alba (Redtop)												
<i>Koeleria cristata</i> (Western Junegrass)..												
<i>Distichlis spicata</i> (Saltgrass)												
Dactylis glomerata (Orchard grass).....												
<i>Poa pratensis</i> (June grass).....												
<i>Poa compressa</i> (Canada bluegrass).....												
<i>Festuca elatior</i> (Meadow fescue).....												
<i>Festuca rubra</i> (Red fescue)												
<i>Bromus*</i> (Brome grasses)												
<i>Agropyron*</i> (Wheat grasses)												
<i>Hordeum jubatum*</i> (Foxtail barley)....												
<i>Elymus condensatus</i> (Giant wild rye) ..												
<i>Plantago lanceolata</i> (English plantain)..												
<i>Rumex Acetosella</i> (Sorrel dock).....												
<i>Chenopodium album</i> (Lambsquarters)...												
<i>Chenopodium glaucum</i> (Goosefoot)												
<i>Allenrolfia occidentalis</i> (Burroweed) ..												
Kochia scoparia* (Burning bush).....												
<i>Atriplex canescens*</i> (Wingscale)												
<i>Atriplex*</i> (Saltbushes)												
<i>Sarcobatus vermiculatus</i> (Greasewood)..												
Salsola Pestifer (Russian thistle).....												
Amaranthus retroflexus (Pigweed)												
<i>Acnida tamarisc.*</i> (West. waterhemp)..												
<i>Iva axillaris*</i> (Poverty weed).....												
Cyclachaena xanthifolia (Burweed).....												
<i>Ambrosia trifida*</i> (Tall ragweed).....												
<i>Ambrosia elatior*</i> (Short ragweed).....												
<i>Amb. psilostach.*</i> (West. ragweed).....												
<i>Franseria acanthicarpa*</i> (Bur ragweed)												
Artemisia tridentata (Sagebrush).....												
Artemisia ludoviciana* (Green sage)....												
Artemisia frigida (Pasture sage).....												
<i>Artemisia*</i> (Mugworts)												
<i>Xanthium pennsylvanicum</i> (Cocklebur)												

* Discussed in the accompanying paragraphs.

common native cottonwoods of the region. Such introduced species as the European white poplar, Carolina cottonwood (*P. Eugenei*) and the Lombardy poplar are planted in the parks and city streets. The cottonwoods on account of their abundance and the enormous quantities of pollen that

most of them produce are probably among the most important trees of the region.

Maples. — The most important species of maple is the boxelder; it is reported to be the commonest tree in Salt Lake City and among those of first rank in the region of Pikes Peak and Colorado Springs. The mountain maple (*Acer grandidentatum* Nutt.) occurs naturally in canyons throughout much of the region, and silver maple (*A. saccharinum*) is planted in city parks and streets. Both species flower in March and April and probably contribute to some extent to the hayfever.

Grasses

Brome Grasses. — Three species of brome grass, *Bromus hordeaceus*, *B. tectorum* and *B. secalinus* are common in the region and are generally reported in hayfever surveys, but it is unlikely that they are of any importance on account of the small amount of pollen that they shed.

Wheat-grasses. — At least seven species of wheat-grass are common in the region and contribute to some extent to the production of hayfever. Bluestem (*Agropyron Smithii*), flowering from June to August, is abundant in the Upper Sonoran and Transition Zones. Thick-spike wheat-grass (*A. dasystachyum* Scribn.) is reported to be important in Salt Lake City and Colorado Springs. Wheat-grass (*A. pseudorepens* Scribn. & Smith) and slender wheat-grass (*A. pauciflorum* Hitch.) are reported for parts of Utah. Bluebunch wheat-grass (*A. spicatum* Scribn. & Smith) and Great Basin wheat-grass (*A. inerme* Rydb.) are abundant throughout much of the region, especially in Utah and to a certain extent in western Colorado. Quack grass (*A. repens*) occurs at various places but is less abundant than the other species and appears to be of no importance.

Foxtail Barley. — *Hordeum jubatum* and meadow barley (*H. nodosum* L.) are widely distributed in this region, and mouseear barley (*H. murinum*) occurs in Idaho and Utah and are probably minor contributing causes of early-summer hayfever.

Other species which probably contribute to a certain extent to early-summer hayfever are the little meadow or short-awned foxtail (*Alopecurus aequalis* Sobol. or *A. aristulatus* Michx.) growing in water or wet places in the Transition Zone almost throughout the region, blue wild-rye (*Elymus glaucus* Buckl.) occurring in meadows of the Transition Zone, brook grass (*Catabrosa aquatica* Beauv.) growing in mountain meadows around springs and along streams in Utah (BARRETT 1934), knot grass (*Paspalum distichum* L.) growing in ditches and recorded in the region of Pikes Peak and Colorado Springs (SERVICE 1934), and the mat grama (*Bouteloua simplex* Lag., *B. procumbens* Griffiths) growing in sandy plains.

Weeds

Burroweed. — *Allenrolfia occidentalis* is recorded by ANDERSON (1930) for parts of Utah. Elsewhere it appears to be unimportant or absent.

Burning Bush. — *Kochia scoparia* is believed to be the most important cause of hayfever throughout most of the inhabited parts of Colorado. Out-

side of the state, however, it appears to be unimportant or absent, though it is recorded for parts of Utah.

Saltbushes. — Besides *Atriplex canescens*, are reported *A. rosea*, *A. hortensis*, *A. hastata*, *A. argentea*, *A. truncata* and *A. confertifolia* as possible contributory causes of hayfever.

Amaranths. — Pigweed is so abundant in weedy places almost throughout the region that it appears to be a factor of considerable importance in hayfever. Its close relatives *Amaranthus blitoides*, *A. palmeri*, and *A. graecizans* also occur and are reported as important local causes of hayfever.

Acnida. — Western water-hemp has only a limited distribution in the region, but is reported by WARING (1925, 1926) to be important in the vicinity of Denver, and by SERVICE (1934) in the vicinity of Pikes Peak and Colorado Springs.

Ragweeds. — The tall, short and western ragweeds occur in this region. Of these only the short is of much importance. In parts of Utah it is considered important by ANDERSON (1930) and is given a third place rating by BARRETT (1934). In the regions of Denver, Pikes Peak and Colorado Springs both the tall and short species occur commonly along roadsides and in waste places but are generally considered less important than Russian thistle and the sagebrushes. Both also occur in the extreme eastern sections of Montana and Wyoming. Western ragweed is still less important though it occurs rather abundantly in about the same parts of the region as the other two species and in Utah.

False Ragweeds. — Besides the bur ragweed which occurs in the Sonoran and Submontane Zones throughout much of the region, the slender ragweed (*Franseria tenuifolia*) occurs in the Sonoran Zone and is reported (BARRETT 1934) as important in Utah.

Sagebrushes and Mugworts. — The common sagebrush is among the worst causes of hayfever in most parts of this region, but it is absent from central and western Montana and western Idaho. Green sage (*A. ludoviciana*) occurs in about the same parts of the region also in western Montana and northern Idaho but is less abundant and less important. Pasture sage (*A. frigida*) occurs in the Sonoran Zone almost throughout and is particularly abundant near cities. Other artemisias which should be mentioned are California mugwort (*A. heterophylla*), gray sage (*A. Wrightii*) and prairie sage (*A. gnaphalodes*) which are common throughout much of the region, and the dragon sagewort (*A. dracunculoides*) which occurs sparingly in the eastern part of the region, and silvery wormwood (*A. filifolia*) which is considered a possible cause of hayfever in the region of Denver.

REFERENCES

The entire Rocky Mountain region has been made the subject of an exhaustive study by STIER, HOLLISTER and BONSER (1930) and reported on together with their study of Washington and Oregon referred to elsewhere (p. 203). These authors furnish a list of all the plants of the region known to cause hayfever and those with hayfever possibilities, giving their time of flowering, their life zones or relative elevations at which they live, and their abundance in the five different ecological districts into which they find the Rocky Mountain region may be divided.

FOSS (1927) reports from Missoula on the hayfever conditions of Montana. He finds that the three hayfever periods there are: 1. March and April due to the pollen of trees, 2. May and June due to the pollen of grasses, 3. July to frost due to the pollen of Russian thistle, sagebrushes and mugworts, and poverty weed, the latter period accounting for over 60 per cent of all hayfever in Montana.

BARRETT (1934) reports a study of the hayfever conditions in and about Salt Lake City. He presents a table of all the plants of the region known to cause hayfever or with hayfever possibilities, together with their periods of bloom, their abundance, and the abundance of their pollen. He also reports the results of counts of atmospheric pollen slides exposed at various places in the state throughout the summer. He finds that: "From the standpoint of pollen production and plant distribution, the most important anemophilous plants of the intermountain states rank as follows: (1) *Gramineae* — grasses (2) *Chenopodiaceae* — Russian thistle, saltbushes, summer cypress [*Kochia*] (3) *Artemisia* — sages (4) *Ambrosiaceae* — ragweeds". Tree hayfever he finds to be caused principally by scrub oak and boxelder; "Nearly half the shade trees lining the streets of Utah towns are boxelders". Grass hayfever he finds to be caused by bluegrass, reedtop, orchard grass, timothy. The late-summer weed hayfever by Russian thistle, the artemisias and ragweeds. The latter, on account of the greater toxicity of their pollen, are more important than the number of and the amount of pollen would suggest. The author also finds that dandelion is an important cause of hayfever: "Four per cent of the hayfever sufferers are sensitive to it. Seven cases have been encountered in which it was the sole or major factor".

ANDERSON (1930), reporting on Utah, gives a classified list of all hayfever plants and those with hayfever possibilities, with their times of flowering and relative importance. He also stresses the observation that dandelion may cause severe hayfever with a few individuals.

TEMPLETON (1924) reports a study of the Sonoran belt of the Intermountain district, the semi-arid non-agricultural part of Utah from 5000 to 7500 feet elevation. The principal trees are found to be junipers and poplars, but these flower before any hayfever begins so can be of no importance. The principal causes of hayfever are found to be the grasses, Russian thistle and other chenopods, and sagebrush.

MULLIN (1922) reporting from Colorado Springs on the hayfever conditions of Colorado, furnishes a list of 66 species of plants known to cause or suspected of causing hayfever, giving their periods of flowering and characteristic habitats; and he emphasizes the fact that hayfever in Colorado is very much a local problem. He finds the principal causes to be Russian thistle, lambsquarters and burning bush among the *Chenopodiaceae*, and the sageworts (*Artemisia*) among the *Compositae*. Ragweed he finds to be important only in and about the cities of the eastern slope of the mountains, while sagebrush and saltbushes are the most important on the western slope. Ragweeds, Russian thistle and other introduced weeds drop out at elevations between 6000 and 7000 feet, but the artemisias ascend to 9000 feet, and sagebrush and timothy even higher. Burning bush, while an important weed at Pueblo, he finds does not occur at Colorado Springs outside of cultivation. But this was in 1922, cf. SERVICE 1934.

WOLF (1924) reporting from Pueblo finds that the chenopods and amaranths are the most important causes of hayfever, the principal species being Russian thistle, burning bush, saltbush, lambsquarters, carelessnessweed and seablite (*Dondia*). Sensitization to one of these he finds implies sensitization to all. Members of the *Artemisia* group are also found to be important in this region, but neither ragweed nor timothy are abundant, and prairie ragweed, though abundant, seems to be unimportant giving reactions with only 5 per cent of the cases tested with its pollen.

WARING (1925, 1926) in association with MAXY POPE reports a survey of the city and county of Denver. The authors furnish a pollen calendar of all the plants known or suspected of causing hayfever. They note that the short, tall and western ragweeds are common along the roadsides. Poverty weed (*Iva axillaris*) is common in low dry places. The common species of *Artemisia* are silvery wormwood and prairie sage (*A. gnaphalodes*). Pasture sage occurs but is not as common here as at lower elevations. The commonest weeds on Denver vacant lots they find are Russian thistle, burning bush, lambsquarters and prairie ragweed. And the pollen most frequently encountered

on their slides are of Russian thistle, burning bush, lambsquarters, tall ragweed, prairie ragweed and bur ragweed.

WARING and POPE (1927) report that the "'cotton', the hair tuft of the seed of the cottonwood tree, is a not uncommon cause of hayfever in Denver". It is, however, not regarded as the primary cause of cottonwood hayfever, serving rather to prolong the hayfever symptoms long after the pollen has ceased to be in the air.

JOHNSON (1938) reporting his experiences with hayfever in Denver, finds tree hayfever, occurring from March to May, to be principally due cottonwoods; grass hayfever, occurring from May to July, to June grass, orchard grass, timothy, wheatgrass, and redtop; weed hayfever, occurring from July to October, to Russian thistle, sages, ragweed and pigweed. He finds that the 'cotton' of the cottonwood trees is a factor in hayfever.

SERVICE (1934) reports a survey of the region of Pikes Peak, Colorado Springs and Manitou. He furnishes a pollen calendar of all hayfever plants and hayfever suspects. He reports that the common trees of this district are boxelder, the cottonwoods (*Populus acuminata*, *P. angustifolia*, *P. Sargentii*, *P. tremuloides*), birch, ash and juniper all of which are common on city streets or in canyons. There are many grasses among which he finds the most important to be redtop, Colorado bluestem (*Agropyron Smithii*), annual bluegrass, June grass, six-weeks grama (*Bouteloua procumbens*). Among the Amaranth-Chenopod group the commonest were found to be western waterhemp, pigweed, lambsquarters, burning bush and Russian thistle. The short, tall and western ragweeds were also found to be very common and the artemisias, especially *Artemisia frigida*, *A. ludoviciana* and *A. tridentata*.

X. Plains and Prairies (North Dakota, South Dakota, Nebraska, Kansas, Minnesota): —

In this region the same three hayfever seasons may be recognized as in the eastern regions, extending through approximately the same periods of the year, but a distinguishing characteristic is that here the ragweeds do not hold universally the position of dominance that they do in the East. This position is disputed with them in parts of the region by Russian thistle, the artemisias, western waterhemp and various other western and southern species. In fact this is the region of transition between the East and the West. DURHAM (1933d) has found that at Pierre, in the central part of South Dakota there is about half as much Russian thistle as ragweed pollen in the air. Westward of this point Russian thistle gains the ascendancy, eastward the ragweeds. The same author finds that western Nebraska is the center of an ever-widening area in which burning bush, a dominant hayfever plant of Colorado, is becoming a serious hayfever menace; at North Platte three fourths of all the chenopod-amaranth pollen in the air is of this species. In the eastern part of the region, however, these plants are unimportant.

Trees

Birches. — Of the several species of *Betula* which occur in this region the most important is the paper or canoe birch. It is the common species in Minnesota, the Dakotas and northern Nebraska. Yellow birch (*B. lutea*) occurs commonly in Minnesota but scarcely elsewhere in the region. Red birch (*B. nigra*) occurs sparingly in swamps and along the banks of streams and ponds in the eastern and southern part of Minnesota. The introduced low birch (*B. pumila*) also occurs in parts of Minnesota, and the eastern gray birch (*B. populifolia*) is recorded by DUKE (1926) in Kansas City,

Table X, HAYFEVER PLANTS OF PLAINS AND PRAIRIES: —
(North Dakota, South Dakota, Nebraska, Kansas, Minnesota)

SPECIES	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
<i>Alnus incana</i> (Speckled alder)				I								
<i>Populus*</i> (Poplars, cottonwoods).....												
<i>Ulmus*</i> (Elms)												
<i>Acer Negundo</i> (Boxelder)												
<i>Acer*</i> (Maples)												
<i>Salix*</i> (Willows)												
<i>Betula*</i> (Birches)												
<i>Fraxinus*</i> (Ashes)												
<i>Celtis occidentalis</i> (Hackberry)												
<i>Quercus*</i> (Oaks)												
<i>Platanus occidentalis</i> (Sycamore)												
<i>Juglans</i> (Walnut, Butternut)												
<i>Carya</i> (Hickories)												
<i>Plantago lanceolata</i> (English plantain).												
<i>Rumex Acetosella</i> (Sorrel dock).....												
<i>Anthoxanth. odorat.</i> (Sw. vernalgrass)..												
<i>Poa pratensis</i> (June grass).....												
<i>Secale cereale</i> (Rye)												
<i>Bromus*</i> (Brome grasses)												
<i>Lolium perenne</i> (Perennial ryegrass)...												
<i>Koeleria cristata</i> (Western Junegrass)..												
<i>Poa compressa</i> (Canada bluegrass).....												
<i>Dactylis glomerata</i> (Orchard grass).....												
<i>Phalaris arundinacea</i> (Reed grass).....												
<i>Phleum pratense</i> (Timothy)												
<i>Agropyron Smithii</i> (West. wheatgrass)												
<i>Agropyron repens</i> (Quack grass)												
<i>Agrostis alba</i> (Redtop)												
<i>Avena fatua</i> (Wild oat)												
<i>Hordeum jubatum</i> (Squirreltail grass)..												
<i>Festuca elatior</i> (Meadow fescue).....												
<i>Beckmannia Sizigachne</i> (Sloughgrass)..												
<i>Cynodon Dactylon*</i> (Bermuda grass).....												
<i>Chenopodium album*</i> (Lambsquarters)												
<i>Amaranthus retroflexus</i> (Pigweed)												
<i>Amaranthus spinosus*</i> (Spiny amaranth)												
<i>Acnida tamarisc.*</i> (West. waterhemp)..												
<i>Salsola Pestifer*</i> (Russian thistle)												
<i>Kochia scoparia</i> (Burning bush).....												
<i>Artemisia filifolia</i> (Silvery wormwood)..												
<i>Artemisia Absinthium</i> (Absinth sage)..												
<i>Artemisia vulgaris</i> (Wormwood).....												
<i>Artemisia Abrotanum</i> (Southernwood)..												
<i>Artemisia caudata*</i> (Tall wormwood)....												
<i>Artemisia ludoviciana</i> (Prairie sage)...												
<i>Artemisia frigida</i> (Pasture sage).....												
<i>Artemisia dracunculoides</i> (Dragon sage)												
<i>Artemisia serrata</i> (Sawleaved mugwort)												
<i>Artemisia biennis</i> (Bienn. wormwood)..												
<i>Artemisia canadensis*</i> (Can. wormwood)												
<i>Artemisia tridentata*</i> (Sagebrush).....												
<i>Artemisia annua</i> (Annual sagewort)....												
<i>Amb. psilostach.</i> (West. ragweed).....												
<i>Ambrosia trifida</i> (Tall ragweed).....												
<i>Ambrosia elatior</i> (Short ragweed).....												
<i>Ambrosia bidentata*</i> (So. ragweed)....												
<i>Iva axillaris</i> (Poverty weed).....												
<i>Iva ciliata*</i> (Rough marshelder).....												
<i>Cyclachaena xanthifolia*</i> (Burweed)....												
<i>Franseria acanthicarpa*</i> (Bur ragweed)												
<i>Xanthium*</i> (Cocklebur)												
<i>Cannabis sativa*</i> (Hemp)												

* Discussed in the accompanying paragraphs.

and other cultivated forms are found commonly about the towns and cities. All flower at about the same time and may occasion a severe type of hay-fever. Besides the birches and alders, other members of the birch family which commonly occur are the hazels (*Corylus americana* and *C. rostrata*) flowering in March and April, the ironwood (*Ostrya virginiana*) and blue-beech (*Carpinus caroliniana*) flowering in April and May.

Maples.— Silver maple (*Acer saccharinum*) occurs rather commonly almost throughout the region, and red maple (*A. rubrum*) principally in the eastern part.

Poplars.— Many species of *Populus* occur in this region. *P. tremuloides*, *P. grandidentata*, *P. deltoides* and *P. balsamifera* are reported by ELLIS and ROSENDAHL (1933) as the most important in Minnesota, and DUKE (1926) reports the necklace poplar (*P. virginiana*) for Kansas City.

Willows.— Many species of *Salix* occur. *S. discolor*, *S. humilis* Marsh., *S. cordata* Muhl., *S. amygdaloides* Anders., *S. fragilis* and *S. alba* are reported by ELLIS and ROSENDAHL but are not regarded as important.

Elms.— The principal species of *Ulmus* are white and slippery elms (*U. americana* and *U. fulva*) which are widely distributed. The Siberian elm (*U. pumila*) and cork elm (*U. racemosa* Thomas) are less common, the latter confined in this region principally to Minnesota and northern Nebraska.

Ashes.— White ash (*Fraxinus americana*), green ash (*F. lanceolata*) and black ash (*F. nigra* Marsh.) occur commonly in Minnesota and to a lesser extent in the Dakotas and Nebraska.

Oaks.— Six species of oak (*Quercus macrocarpa* Michx., *Q. velutina*, *Q. ellipsoidalis* E. J. Hill, *Q. borealis*, *Q. coccinea* and *Q. alba*) are recorded by ELLIS and ROSENDAHL as common and likely to cause hayfever in Minnesota. The same species, however, also occur to a certain extent elsewhere in the region.

Grasses

This is primarily a region of grasses. In them lie the great inherent riches of the plains and prairies, yet the grasses are no more important as causes of hayfever here than elsewhere for the native species are nearly harmless. It is the introduced weeds and agricultural grasses that have to be reckoned with. GATES (1937) in his delightful little book on the grasses of Kansas states: "The pollen of certain grasses causes hayfever in human beings. Chief among these grasses in Kansas are orchard grass (*Dactylis glomerata*), bluegrass (*Poa pratensis*), meadow fescue (*Festuca elatior*), rye or ray grass (*Lolium perenne*), western wheat grass (*Agropyron Smithii*), rye (*Secale cereale*), tall oatgrass (*Arrhenatherum elatius*), timothy (*Phleum pratense*), redbtop (*Agrostis alba*), Bermuda grass (*Cynodon Dactylon*), sweet vernalgrass (*Anthoxanthum odoratum*), Johnson grass (*Sorghum halepense*), and corn (*Zea Mays*)". It is interesting to note that of all these only western wheatgrass is native to the state, and it is among the least important of the list.

Brome Grasses.— *Bromus inermis*, *B. secalinus*, *B. ciliatus* L. and

B. hordeaceus are common throughout much of the region but are of little or no importance.

Fescue Grasses. — Besides meadow fescue are found about ten other species. Of these six-weeks fescue (*Festuca octoflora*) and sheep fescue (*F. ovina*) are widely distributed and regarded by ELLIS and ROSENDAHL as having hayfever possibilities.

Bermuda Grasses. — *Cynodon Dactylon* occurs only in Kansas, and in parts of the state appears to be a factor to be reckoned with. Johnson grass occurs in fields and waste places in Kansas and is even sometimes cultivated in the southern part, but it does not appear to be an important factor in hayfever.

Weeds

Russian Thistle. — *Salsola Pestifer* is an important cause of hayfever throughout all this region except the northern and eastern parts of Minnesota, and accounts for possibly 20 per cent of the hayfever. Its prevalence is largely due to excessive grazing and other mismanagement of the soil. Since its introduction it has come to possess a large part of the land which was formerly occupied by native prairie grasses.

Spiny Amaranth. — *Amaranthus spinosus* occurs throughout the region but only in the southern part is it abundant enough to be a factor of importance; it is recorded by DUKE and DURHAM (1924) as a possible cause of hayfever in Kansas.

Waterhemp. — Two species of *Acnida* occur in this region. By far the most important is the western waterhemp (*A. tamariscina*). It is extremely abundant in Kansas but does not extend in effective quantities northward. Instead it is replaced by its less important relative *A. tuberculata*, rough-fruited waterhemp.

Docks. — Besides the sorrel docks several other species of *Rumex* occur. ELLIS and ROSENDAHL (1933) record curly dock, peach leaved dock (*R. altissimus* Wood), golden dock (*R. persicarioides* L.), pale dock (*R. mexicanus* L.), bitter dock (*R. obtusifolius*) and the great water dock (*R. britannica* L.).

Mugworts and Wormwoods. — *Artemisias* are among the most important causes of hayfever in the region. RYDBERG (1932) describes 30 species occurring. Those listed in the flowering calendar, except the first and last, are regarded by ELLIS and ROSENDAHL (1932) as important; common sagebrush occurs only in the extreme western part of the Dakotas and Nebraska and the sand sagebrush in the western part of Kansas, where they may be of some local importance. *Artemisia canadensis* is a northern species only entering the region along the Canadian border, but it is believed to be of local importance in northern Minnesota. *A. caudata* and *A. dracunculoides* are the commonest species, growing in sandy soil, especially on dry slopes and sandy outwash plains, and in vacant lots and waste places within the cities. ELLIS and ROSENDAHL (1932) state that the three introduced species *A. Abrotanum*, *A. vulgaris* and *A. Absinthium* have become naturalized to some extent in Minnesota and the eastern part of the Dakotas. They are also frequently grown as ornamentals, the first used as a hedge

plant on account of its robust character, and for this reason hayfever patients are liable to come in very close contact with them.

Ragweeds and False Ragweeds. — The tall, short and western ragweeds are extremely abundant throughout the entire region and generally speaking their pollen constitutes the worst cause of hayfever. The southern or lance-leaved ragweed is a plant of the southern prairies, abundant in Kansas and occurring as far north as southern Minnesota, but not recorded for the Dakotas. RYDBERG (1932) records four species of *Franseria* for this region. Of these *F. acanthicarpa* is widespread in the Dakotas but occurring only sporadically elsewhere. *F. tenuifolia*, *F. discolor* and *F. tomentosa* also occur in parts of the region but appear to be unimportant. Prairie ragweed (*Cyclachaena xanthifolia*) is most important in the Dakotas and Nebraska but occurs more or less abundantly throughout. Rough marsh-elder (*Iva ciliata*) is a southern species and occurs in this region only in Kansas and southern Nebraska.

Cocklebur. — Three species of *Xanthium* are widespread, frequenting low moist places, sandy shores and alluvial bottom lands, fields and waste-places. One of the commonest is the great clotbur (*X. speciosum*) which is a particularly heavy pollen shedder. Beach clotbur (*X. echinatum* Murr.) and common cocklebur (*X. pennsylvanicum*) are also common.

Hemp. — *Cannabis sativa* is abundant throughout, and is stated by DURHAM (1933*d*) to outrank ragweed in some areas along the Mississippi and Missouri Rivers, but Omaha is the only place investigated where it assumes allergic importance. The reason for its abundance in some parts of Nebraska, as pointed out by MACQUIDDY (DURHAM 1935*b*), is that in about the year 1889 hemp was introduced into this region for making rope. It was first cultivated at Fremont, Nebraska, later at Omaha, Lincoln and Columbus. Though it is no longer cultivated, it has escaped and now ranges widely from these places.

REFERENCES

The first study of the hayfever conditions of any part of this region appears to be that of DUKE and DURHAM (1924), "A Botanic Survey of Kansas City and Vicinity". They find that the most important trees are boxelder, sycamore, cottonwood, ash, hazel, black walnut, hickory and oak, their flowering periods extending from March to June but occurring mostly in April and May. The most important grasses they find to be rye, June grass, timothy, slough grass and orchard grass, flowering from the middle of May to the middle of July. Sudan grass and Johnson grass, while they occur, are found to be unimportant. Among the weeds, flowering mostly from mid August to frost, they found the most important to be the short and tall ragweeds, ranking far ahead of all others, and of lesser importance, southern ragweed, Russian thistle, burning bush and wormwoods.

DUKE (1926) furnishes a pollen calendar for Kansas City accompanied by descriptions and photographic illustrations of all the most important hayfever plants.

A series of exhaustive researches into the pollen situation in Minnesota and the Dakotas has been conducted by ELLIS and ROSENDAHL (1932, 1933, 1934). In the first of these studies, which deals only with late-summer hayfever, the authors furnish a list, with their times of flowering, of all species comprising the ragweed and wormwood groups and giving the importance and distribution of each within the three states. They find that all of the many species of *Artemisia* are important, and that reactions of hayfever sufferers to their pollen are more severe than to that of ragweed, and, with many

cases, allergenically distinct. The most important ragweeds they find are the tall and short. The western ragweed is found scattered throughout the area on sandy soils in fields, pastures and open situations, and occasionally in openings in the northern coniferous forest, enjoying the widest distribution of all the ragweeds in the region. It is liable to be a source of trouble to patients who seek the north woods for relief. Next in importance to the ragweeds is found to be prairie ragweed. In the second paper which deals with the hayfever situation in Minnesota during all seasons, the authors furnish a list of all plants with hayfever possibilities, their dates of flowering and relative abundance. The species are assembled according to their biological relationships into 24 groups which may be used in combination for diagnosis and treatment instead of the individual species. It is found that the ragweed group, containing the ragweeds, bur ragweed, prairie ragweed and cocklebur, is the most important; the sage-wormwood group, containing all the artemisias, is next in importance; then follow the groups of grasses and of pigweeds. The oak, elm and ash groups are found to be the most important among the trees, but all much less so than the groups just mentioned. The third paper of these authors deals with the diagnosis and treatment of hayfever with special reference to Minnesota. They furnish 60 maps showing the distributional abundance within the state of 60 species of hayfever plants. They find that the importance of the dock group, including various species of *Rumex*, *Polygonum* and *Rheum*, is probably greater than has generally been recognized. Approximately 20 per cent of the hayfever cases studied were found to be sensitive to pollen of this group. But the most important group is that of the ragweeds, and the authors find that several members of this group are extending their range and are becoming established in localities where they were formerly unknown.

ROSENDAHL, ELLIS and DAHL (1940) continuing this work, report a four-year study of "Air borne Pollen in the Twin Cities Area with Reference to Hayfever". They list all the important groups of hayfever plants and furnish graphs showing their pollen concentration throughout the season.

STOSSER (1942) reports from Minneapolis a study of hayfever in 413 children. Of these 306 were found to be sensitive to ragweed, 209 to the sage-mugwort group, 146 to Russian thistle, 72 to grasses, and fewer to the trees, plantain and other weeds.

VAUGHAN (1931) furnishes a pollen calendar of the hayfever plants of Kansas City compiled by DUKE (1926), and of the Prairies and Plains compiled by BALYAT (1930). HANSEL (1936) presents a brief but comprehensive summary of the published reports dealing with the hayfever conditions in the Plains and Prairies.

WALTON (1939, 1940) and WALTON and DUDLEY (1940) have recently reported the results of their studies in Manitoba and western Canada. They find that the early hayfever season begins about April 20, and is due to the poplars, hazels, willows, birches, boxelder, elm, ash and scrub oak. Summer hayfever begins in June, and is due to the grasses and plantain. The ragweed pollen counts they find to be low but the sages and Russian thistle are important in the fall.

GLOSSARY

Allergen. — A substance which produces an allergic manifestation in an allergically sensitized human being.

Allergy. — A specific hypersensitiveness among human beings regardless of its cause or origin. Such maladies as hayfever, asthma, urticaria, angioneurotic oedema, some forms of eczema and migraine are among the commonest manifestations. Dermatitis from poison ivy, primrose and other plants is included by some allergists, as indeed, is indicated by the above definition, though such is excluded by other allergists.

Amphiphilous. — Pollinated by the agencies of both insects and wind, as with willows and some maples.

Anemophilous. — Pollinated by the agency of wind, as in pine and ragweed.

Annual. — Flowering and fruiting in the first year or season and then dying, as in short ragweed and Russian thistle.

Anther. — The sac or sacs containing the pollen, the essential part of the stamen.

Aperture (pollen). — *See* Germinal aperture.

Appressed. — Adpressed, lying close and flat.

Arachnoid. — Cobwebby, of slender entangled hairs.

Aspidate (pollen). — With pores surrounded by shield-shaped thickenings.

Awn. — A slender bristle at the end of an organ, in the grasses a continuation of the midnerve of a glume or lemma.

Axil. — The upper angle formed by a leaf or branch with the stem.

Axillary. — Borne at or pertaining to an axil.

Bipinnatifid. — Twice pinnatifid.

Biennial. — Lasting two years, flowering and fruiting in the second, as in carrot.

Canescent. — Grayish white or hairy, the surface covered with fine white hairs

Calyx. — The outer perianth of a flower.

Carpel. — A simple pistil or one member of a compound pistil.

Catkin. — Ament. A scaly deciduous spike of flowers.

Cespitose. — Growing in tufts.

Connective. — The filament or tissue connecting the cells of an anther, particularly when the cells stand apart from each other.

Corolla. — The inner perianth of a flower.

Corymb. — A flat-topped or convex open flower cluster, with pedicels of unequal length, progressing in its flowering from the margin inward.

Cotyledon. — Seed leaf.

Culm. — The jointed stem of a grass, which is usually hollow except at the nodes.

Cyme. — A flattish flower cluster in which the terminal or central flowers bloom first.

Deciduous. — Falling away at the close of the growing period.

Decumbent. — Reclining, but with the summit ascending.

Dentate. — Toothed with the teeth standing directly outward.

Digitate. — Parted or divided like the fingers of the hand, applied usually to the palmate division or lobing of leaves.

Dioecious. — Having only distinct staminate and pistillate flowers, and these borne on separate plants, as in poplars and willows.

Disk. — In *Compositae* the tubular flowers collectively, as distinct from the ray flowers.

Entire. — Margin not toothed or indented in any way.

Entomophilous. — Pollinated primarily by the agency of insects, as in orchids, sweet peas and goldenrods.

Exine. — The outer wall of a pollen grain.

Fascicle. — A close bundle or cluster.

Filament. — The part of a stamen which supports the anther.

Floret. — A small flower, one of a cluster, as the individual flowers of the heads of *Compositae*; the lemma and palea with included stamens and pistil among the grasses.

Furrow (pollen). — *See* Germinal furrow.

Germinal aperture. — A hole in the furrow membrane or exine through which a pollen tube may emerge.

Germinal furrow. — A groove or elongate opening in the exine of a pollen grain, either enclosing a germ pore or serving directly as the place of emission of the pollen tube.

Germinal papilla. — A dome-shaped protrusion through a germinal aperture of a pollen grain; the pollen tube "Anlage".

Germ pore. — *See* Germinal aperture.

Glomerule. — A compact or condensed head-like cyme.

Glumes. — The pair of bracts at the base of a spikelet among the grasses.

Halophyte. — A plant growing in salty or alkaline soils, as pickleweed, greasewood.

Herb. — A plant with no persistent woody stem above ground.

Herbaceous. — Having the characters of an herb; leaf like in color and texture.

Hyaline. — Transparent or translucent.

Intine. — The inner wall of a pollen grain.

Involucre. — A circle of bracts subtending a flower cluster.

Laciniate. — Cut or shredded into narrow divisions.

Lemma. — The bract of a spikelet above the pair of glumes among the grasses.

Lenticels. — Small areas in the bark where the cork cells are somewhat loose and spongy allowing a small amount of gas interchange between the tissues below and the air outside.

Lodicule. — Among the grasses, minute hyaline scale-like organs at the base of the stamens whose function is the opening of the floral envelope at anthesis.

Monoecious. — Having only distinct staminate and pistillate flowers, and these on the same plant, as in walnuts, pines and ragweeds.

Mucronate. — Tipped with a short soft spine.

Node. — The place upon the stem which normally bears a leaf or leaves; among the grasses, a joint of the culm.

Operculum. — A thickening of measurable bulk and clearly defined of the pore membrane of a pollen grain, as in that of grass.

Ovary. — The part of the pistil that contains the ovules.

Palet, Palea. — The upper bract which, with the lemma, incloses the flower among the grasses.

Palmate. — Radiately lobed or divided, as of a leaf.

Panicle. — A loose irregularly compound inflorescence with pedicillate flowers.

Papilionaceous (corolla). — Butterfly shaped, having a standard, wings and keel, as in sweet pea and locust.

Pedicel. — Stem of a flower in a flower cluster.

Peduncle. — Stalk or stem of a flower or flower cluster.

Peltate. — Shield shaped, and attached to its stalk inside its margin.

Perennial. — Lasting year after year, as in western ragweed, Bermuda grass and sagebrush.

Perfect (flower). — Having both pistil and stamens, as in rose or privet.

Perianth. — The floral envelope, consisting of the calyx and corolla or calyx alone.

Petiole. — Stalk of a leaf.

Pinnate (leaf). — Compound, with the leaflets arranged on each side of a common petiole.

Pinnatifid. — Cleft in a pinnate manner.

Pistil. — A seed-bearing organ.

Pore. — *See* Germinal aperture.

Pubescent. — Clothed with soft downy hairs.

Raceme. — A simple inflorescence of pedicellate flowers upon a common more or less elongate axis.

Rachilla. — A small rachis. Among the grasses applied especially to the axis of a spikelet.

Rachis. — The axis of a spike or raceme, the prolongation of the peduncle through the flower cluster; the axis or midrib of a compound leaf; among the grasses the main axis and branches of an inflorescence on which the spikelets are borne.

Ray. — In the *Compositae*, the ligulate corolla of a marginal flower.

Receptacle. — The more or less expanded or produced portion of an axis which bears the organs of a flower or (in the *Compositae*) the collected flowers of a head.

Rhizome. — Underground stem; rootstock.

Rootstock. — Rhizome.

Scaphoid. — Boat shaped.

Sessile. — Without a stalk.

Spike. — An unbranched inflorescence in which the units are more or less sessile along a central axis. Ordinarily the units are individual flowers as in plantain, but among the grasses they are spikelets as in timothy, and among the *Compositae* they are flower heads as in ragweed.

Spikelet. — A secondary spike; among the grasses the unit of inflorescence, consisting of two glumes and one or more florets.

Stamen. — A pollen bearing organ.

Stigma. — The part of the pistil receptive to pollen grains and on which they germinate, usually the apex of the style.

Stipules. — Small supplementary organs or appendages of a leaf, borne in pairs at the base of the petiole.

Strobile. — Cone.

Style. — The portion of a pistil between the ovary and stigma, generally contracted and often slender.

Tomentose. — Densely pubescent with matted wool.

Tricolpate (pollen grains). — Possessing three meridionally arranged germinal furrows.

Trischistoclastic. — The system in which the furrows of pollen grains of the higher dicotyledons tend to form, characterized by triconvergent angles.

Whorl. — An arrangement of leaves or other organs in a circle round the stem.

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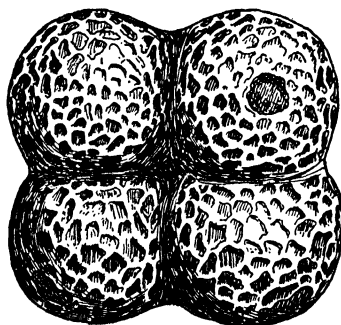
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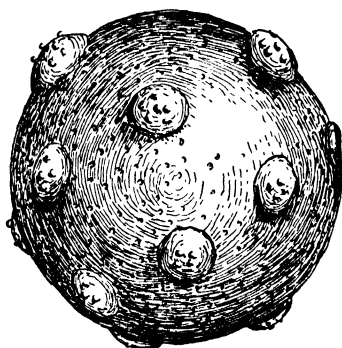
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Chronica Botanica

Chronica Botanica, an international collection of studies in the method, philosophy, and history of biology and agriculture, aims at the promotion of (1) international relations in the plant sciences, (2) studies in the history, method, and philosophy of biology and agriculture, (3) a better understanding between specialists in various branches and their relations with the outside world.

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► An *International Plant Science Addressbook and Register*, to be published as soon as possible after the War, in parts in CHRONICA BOTANICA, is in preparation. This will include a fifth edition of our World List of Plant Science Institutions and Societies and, after revision, much of the material submitted for the Int. Addressbook which we were preparing in the unfortunate summer of 1939 (considerable parts of this have still been published in spite of the war in CHRONICA 6, nos. 12 and 13 and CHRONICA 7, no. 3).

► In forthcoming volumes of the CHRONICA we will publish an extensive, critical, biographical dictionary of plant scientists of all times. A detailed note about this *Index Botanicorum*, which is being prepared with the assistance of the Arnold Arboretum of Harvard University, has been published in the Autumn Number of CHRONICA BOTANICA for 1944. Reprints of this article (with detailed notes for contributors) are available upon request.

... more valuable to the botanical world under present conditions than even in normal times (NATURE).

A remarkable achievement of editorial effort and co-operation . . . it covers a field not hitherto pre-empted, conflicts with no established periodical, supplements those already in existence, and should by its very name, encourage the spirit of international co-operation (JOURNAL OF BOTANY).

Die Botanik kann sich eines Organs rühmen, das bisher keine andere Wissenschaft kennt und das letzten Endes nichts mehr und nichts weniger bezweckt als eine Besinnung der Botaniker auf sich selbst als Glieder einer durch den Arbeitsgegenstand verbundenen internationalen Gemeinschaft (ZEITSCHRIFT FÜR BOTANIK).

The first three volumes of CHRONICA BOTANICA (1935/37) were published as annual records and reviews of current research, activities and events in the plant sciences. Vols. 4-7 (1938-1942) were published in periodical form, with the subtitle "the international plant science newsmagazine." From vol. 8 (1944) onwards CHRONICA BOTANICA contains more material than previously dealing with the basic humaniors of the plant sciences: history, methodology and philosophy. Much space, however, continues to be given to short discussions, news of all kinds, reviews, notices, etc. Every autumn we intend to publish a special number (*Chronica Botanica Calendar*) entirely devoted to material of a timely interest, including such sections as *International Affairs*, *The Forum*, *Quotations*, *The Chronicle*, *Serta Biographica*, *Reviews and Notices*.

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● Autumn 1944 Catalogue ●

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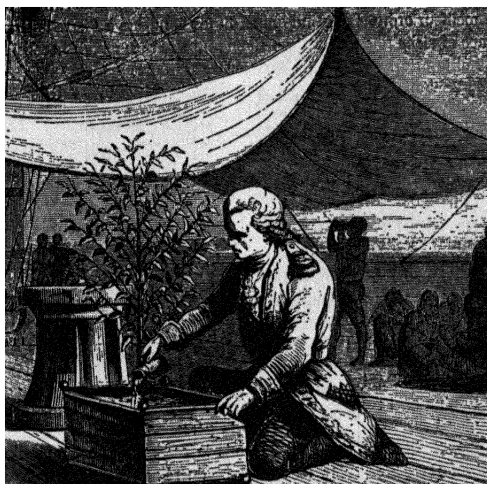
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► **FOREST TREE SEED OF THE NORTH TEMPERATE REGIONS** by H. I. Baldwin (N. Hampshire Forestry Dept.).—The first modern book dealing exclusively with tree seed in English. With a polyglot glossary of tree seed terms.—*A New Series of Pl. Sci. Books, Vol. 8* (1942); Sup. roy. oct., buckram, 240 pp., 28 illustr.....\$4.75

Contents: Structure and development. Seed production. The importance of seed source or provenance. Seed collection. Extraction. Cleaning and treatment. Storage and longevity. Insects, diseases and other enemies. Germination. Internal and external factors affecting germination. Chemical aspects. Seed stimulation. Different kinds of tests. Purity analysis. Determination of origin. Testing viability without germination. Testing of germination. Seed testing stations and certification. Research. Glossary. Indices.

The material presented is critically examined, well documented, and there are fairly extensive lists of references to literature. Much of the discussion on harvesting, storage, and germination pertains with equal validity to many types of plants, so that the book has a wide field of interest and usefulness beyond the more immediate limits of species of trees (KRAUS in BOT. GAZETTE).

The work will be indispensable to research workers in the field of tree seed and very useful to practical foresters and members of the seed trade. It is not a handbook of tree seed, giving cut and dried information about individual species, but a reference book and a guide, not only to existing knowledge but also to the directions in which that knowledge should be extended in the future (THOMSON in NATURE).

► **PLANT VIRUSES AND VIRUS DISEASES** by F. C. Bawden (Rothamsted Experimental Station).—*Second entirely revised and modernized edition* with many new illustrations. No chapter remains unchanged, and more than half have been completely rewritten. Recent advances in all branches of the subject are described and correlated. Techniques new to botanists are discussed, special attention being given to work on the chemical, physico-chemical and serological properties of purified virus preparations. Modern concepts on the nature, origin, size and multiplication of viruses are critically reviewed.—*A New Series of Pl. Sci. Bks., Vol. 13* (1943); Sup. roy. oct., buckram, 294 pp., 48 illustr.....\$4.75

Contents: Symptomatology. Transmission. Relationships between viruses and insect vectors. Virus strains, mutation, and acquired immunity. Serological reactions. Methods of purification. Properties of purified virus preparations. Optical properties of purified virus preparations. Inactivation of viruses. The sizes of virus particles. Physiology of virus-diseased plants. The classification of viruses. Control. Origin and multiplication of viruses.

In recent years students of plant viruses have been joined by workers in subjects which at first sight seem to have little connection with plant pathology. Biochemists, physical chemists, serologists, statisticians and X-ray specialists have all taken a hand in the game and the ordinary biologist finds himself somewhat bewildered by these specialists each talking a jargon of his own. One welcomes therefore the present volume which gives a lucid explanation of much of this unfamiliar technique . . . written in an interesting and readable style and the subject is presented in a coherent and accessible manner and is not a mere statement of unrelated facts (K. M. SMITH in J. PATH. BACTER.).

This second edition is a useful and welcome compilation. Since the research on plant viruses has contributed so much to an understanding of their fundamental nature, this book is valuable to the animal as well as to the plant biologist. It is a fine tribute to British appreciation of fundamental science that this excellent work has been continued while bombs were falling (RIKER in BOT. GAZETTE).

► **A SOURCE BOOK OF AGRICULTURAL CHEMISTRY** by C. A. Browne (U. S. Dept. of Agriculture).—A History of Developments in the Application of Chemistry to the Theory and Practice of Agriculture from the Time of DEMOCRITUS to the Period of LIEBIG.—*Chronica Botanica, Vol. 8, No. 1* (1944); Sup. roy. oct., 290 pp., 1 plate, 32 illustr.....\$5.00

Contents: Agricultural chemistry in ancient times. Agricultural chemistry in the alchemical and iatrochemical periods. Agricultural chemistry in the time of the early Royal Society. Agricultural chemistry in the early phlogiston period. Agricultural chemistry in the late phlogiston period. Agricultural chemistry during the chemical revolution. Agricultural chemistry at the beginning of the modern period.

This is a history-of-science reference book which gives a chronological account of attempts to apply chemical principles to the interpretation of the phenomena of plant and animal life in some of their relations to agriculture. After an introduction defining the scope and aims of agricultural chemistry the development of this science is traced in seven chapters beginning with the ancient Greek and Roman era and then continuing through the alchemical and iatrochemical periods, the time of the early Royal Society, the phlogiston period and the chemical revolution, to the beginning of the modern period in the mid-nineteenth century. Brief accounts are given of the lives, researches, and publications of fifty different investigators with special stress upon the influences they exercised on subsequent developments. Thirty-two illustrations, from classic publications, of apparatus and processes, of title pages and specimens of text and of historic tabulations, assist the reader in following the explanations of the different chapters. Translations are given of pertinent passages and each biographical sketch is followed with a list of references to original source material. A subject index and an author index facilitate the location of special topics. Following the indices is an addendum giving references to later source material for the guidance of those who desire to study more recent developments during the past century.

► **THOMAS JEFFERSON AND THE SCIENTIFIC TRENDS OF HIS TIME** by C. A. Browne (U. S. Dept. of Agriculture).—A scholarly essay, by the Nestor of American Agricultural Chemists, on THOMAS JEFFERSON's position in the world of science, his "Notes on the State of Virginia", his scientific services to the new republic of the United States, his agricultural and educational work, and some of the eminent contemporaries who knew JEFFERSON personally and exchanged with him letters that throw much light on the scientific movements of the time.—*Chronica Botanica, Vol. 8, No. 3* (1944); Sup. roy. oct., 64 pp., illustrated with 17 contemporary drawings, maps, and facsimiles.....\$1.25

JEFFERSON's natural inclinations were more toward science than toward politics and though the trend of events caused his career to fall in the latter field he strove as resolutely to create a democracy of science as he did to establish a democracy of government. The publication is timely in view of the recent commemorations of the bicentenary of JEFFERSON's birth.

► **PRINCIPLES OF PALEOBOTANY** by William C. Darrah (Harvard U.).—*A New Series of Pl. Sci. Bks., Vol. 3* (1939); Roy. oct., 239 pp., 7 pl.; out of print, a new edition is in preparation for publication after the war.

Eine wertvolle übersichtliche Darstellung unseres heutigen paläobotanischen Wissens . . . Die Gliederung, sowohl hinsichtlich der Pflanzenformen als auch der Pflanzengesellschaften in den einzelnen geologischen Zeitepochen zeigt von universeller Beherrschung des Forschungsgebietes (HOFMANN in ORT. BOT. Z.).

This book was written for the unspecialized botanical reader. It is in no way, however, a popularized account . . . the author's enthusiasm is so evident that it may go a long way to inspire keenness (HARRIS in NATURE).

► **AN INTRODUCTION TO POLLEN ANALYSIS** by G. Erdtman (Västerås, Sweden). Foreword by Roger P. Wodehouse, author of 'Pollen Grains'.—The first and only comprehensive reference work on the methodology and applications of pollen analysis.—*A New Series of Pl. Sci. Bks., Vol. 12 (1943)*; Sup. roy. oct., buckram, 239 pp., 46 plates and illustr.\$5.00

From the contents: Historical. Chemistry of Pollen. Pollen Preparations. Preparation of Fossil Pollen-Bearing Material. Pollen and Spore Morphology. Graphic Presentation. Correlation. Output and Dissemination of Pollen. Surface Samples. Pollen Flora of Peat Samples. Investigations in different Countries. Tertiary Deposits. Honey and Drugs.

An account of the principles and methods used in research on pollen, especially fossil pollen. The author has brought together and evaluated all previous work and greatly extended it through his own researches. A large part of the book is devoted to morphology of the pollen grains of angiosperms and gymnosperms, and of the spores of ferns, stressing the means of their identification in the fossil form. This is greatly facilitated by several hundred original drawings from both fossil and living materials. The author shows the practical application of pollen identification in palaeoclimatology, archaeology, forestry and phytogeography and other fields. His studies of pollen production and dissemination together with studies of modern pollen deposits point the way to a very realistic reconstruction of the past through studies of ancient pollen deposits.

Deeply buried in ancient bogs are the records of the climates that prevailed during the years of their slow filling up. For the climates determined the nature of the forests in the vicinity, and the forests shed pollen on the mud and shallow water, year after year; so that now a properly trained botanist can accurately describe long-vanished forests by peering through his microscope. This branch of paleoecology looks easy but isn't; how to master its difficulties and avoid its pitfalls can be learned from 'An Introduction to Pollen Analysis' by G. ERDTMAN, Swedish master of this tedious but rewarding technique (SCIENCE NEWS LETTER).

► **THE GENUS BAZZANIA IN CENTRAL AND SOUTH AMERICA** by Margaret Fulford (Univ. of Cincinnati).—A critical monograph of one of the most interesting genera of liverworts, the first complete modern revision of the neotropical species of a large and difficult genus of hepaticae, since STEPHANI produced his confusing *Species Hepaticarum*.—*Ann. Crypt. et Phytop.*, Vol. 3; Roy. oct., ca. 240 pp., 59 plates, in press.\$5.00

► **ROOT DISEASE FUNGI** by S. D. Garrett (Rothamsted Experimental Station).—The first book dealing exclusively with this important group of fungi. Principles of root disease control are fully expounded for the benefit of all practising plant pathologists. Control measures are classified separately for field, plantation and glasshouse crops. A special feature is the full treatment of root disease control in tropical and sub-tropical crops, but no important root disease of any crop has been omitted. Of particular interest to soil microbiologists will be the chapters on biology and evolution of the root-infecting fungi.—*Ann. Crypt. et Phyt.*, Vol. 1; Roy. oct., cloth, ca. 175 pp., 10 illustr., in press, ready autumn 1944.\$4.50

Contents: Parasitic specialisation in the root-infecting fungi. Parasitic activity. Influence of soil temperature. Influence of soil moisture content, texture and reaction. Influence of soil organic content and concentration of plant nutrients. Saprophytic activity of the root-infecting fungi. Dormancy. Control in field crops: crop rotation, plant sanitation, disease control under the growing crop. Control of root disease in plantation crops: on virgin areas; in mature plantations and on replanted areas; special problems; glasshouse crops.

► **WOOD PULP** by Julius Grant, Author of 'Books and Documents', etc.—A concise treatise of the origin, manufacture, testing, uses, and economic importance of

wood pulp.—*A New Series of Pl. Sci. Bks., Vol. 2 (1938)*; Roy. oct., 209 pp.; out of print. It is planned to deal again with the subject matter of this book in a forthcoming volume on wood chemistry and related subjects.

► **THE CYTOPLASM OF THE PLANT CELL** by Alexandre Guillaumond (Sorbonne), authorized translation from the unpublished manuscript by Lenette Rogers Atkinson. Foreword by William Seifriz.—A critical review of our present knowledge of the cytoplasm and its morphological constituents by the eminent French cytologist.—*A New Series of Pl. Sci. Bks., Vol. 6 (1941)*; Sup. roy. oct., buckram, 247 pp., 152 illustr.\$4.75

Contents: General Facts on the Structure of the Plant Cell, its Cytoplasm and Morphological Constituents. The Physical Properties and General Characteristics of the Cytoplasm. Chemical Constituents. Physico-Chemical Constituents of the Cytoplasm. The Plastids. The Chondriome. The Relationship between Chondriosomes and Plastids. Duality of the Chondriome. Hypotheses Relative to the Role of Chondriosomes and Plastids. The Vacuoles. Vital Staining of the Vacuoles. Development of the Vacuolar System. Origin and Significance of the Vacuoles. The Role of the Vacuolar System and Hypotheses concerning it. Golgi Apparatus, Canaliculi of Holmgren and other Cytoplasmic Formations. Lipide Granules, Microsomes and other Metabolic Products. Cytoplasmic Alterations.

The present volume is the first addition, printed in America, to the list of books which Dr. FRANK VERDOORN is editing and publishing under the title, *A New Series of Plant Science Books*. Mrs. ATKINSON has accomplished an excellent job of translating and interpreting for English readers a highly stimulating work, which can be recommended to botanists generally (BEAL in BOT. GAZETTE).

This book gives a thorough, critical and well-balanced survey of the various theories on cytoplasm, chondriosomes, plastids, vacuoles, etc., in which both the morphological and the functional (physico-chemical) point of view have been adequately stressed. Though the author, as one of the leading cytologists, has his own pronounced view, he always does justice to contrary views, so that a very high degree of objectivity in the treatment is obtained (LÜTJENHARMS in J. S. Am. Bot.).

► **LECTURES ON THE INORGANIC NUTRITION OF PLANTS** by D. R. Hoagland (Univ. of California).—This series of lectures, based on the *Prather Lectures at Harvard University*, delivered by the author in the spring of 1942, outlines a number of important problems of plant nutrition, with a very considerable amount of illustrative material derived from extensive researches at the Univ. of California. Scientific aspects of certain soil-plant interrelations, nutrient absorption and utilization, and artificial culture methods are primarily discussed. Trends of research in plant nutrition and opportunities for further exploration are stressed. The discussions have been prepared with consideration given to the broad interests of plant scientists who are not specialists in the subjects presented, but who wish to learn of the nature of problems of plant nutrition, especially of recent advances in this field, as they may have a bearing on related fields of research.—*A New Series of Pl. Sci. Bks., Vol. 14 (1944)*; Roy. oct., buckram, 226 pp., numerous ill., tables and plates\$4.00

Contents: A survey of problems. Micronutrient chemical elements and plant growth. The absorption and accumulation of salts. Upward movement and distribution of inorganic solutes. The growth of plants in artificial media. Some biochemical problems associated with salt absorption. Aspects of the potassium nutrition of plants as illustrating problems of the system, soil-plant-atmosphere.

The book is especially valuable as there does not exist a general account of recent advances in the subjects discussed, though important progress has been made in recent years, in our

knowledge of plant nutrition. Advances in this field are of interest not only to the plant physiologist, but also to the general physiologist, the agronomist, horticulturist, plant pathologist and soil scientist.

► **FUNGICIDES, STUDIES IN THE DYNAMICS OF FUNGICIDAL ACTION** by J. G. Horsfall (Connecticut Agric. Experiment Station).—An examination of the physics and chemistry of the mechanisms by which fungicides control plant diseases. Pertinent data are reviewed and critically discussed in the light of a relatively new tool for assay; namely, dosage-response. An analysis is given of the problem of deposition, coverage and tenacity as factors in protection. A discussion is also given of the factors in chemotherapy, synergism, and modes of toxic action, for copper and sulphur, fungicides. The book ends with a chapter on the new organic fungicides and phytotoxicity. — *Ann. Crypt. et Phyt.*, Vol. 2; Roy. oct., cloth, ca. 240 pp., 20 illustr., in press, ready winter 1945....\$5.00

Contents: Historical introduction. Some general concepts. Laboratory assay. Some problems of data assessment. Principles of chemical protection. Deposition. Coverage of single surfaces. Coverage of multiple surfaces. Tenacity. Chemotherapy. Action of copper. Action of sulfur. Action of organic nitrogen compounds. Action of other organic compounds. Antagonism and synergism. Phytotoxicity.

► **BIOLOGICAL FIELD STATIONS OF THE WORLD** by Homer A. Jack, Ph. D.—An extensive and critical study of the aims, scope and organization of the biological field stations of the world. A unique account of great practical, as well as historical interest. Based on the results of years of travel and world wide systematic enquiries. — *Chronica Botanica*, Vol. 9, No. 1; Sup. roy. oct., ca. 90 pp., illustrated, in press, ready autumn 1944.....\$2.50

From the contents: Purpose of biological stations. History. Location. Administration. Equipment. Living Facilities. Instruction. Educational Philosophy. Research. Annotated list of biological stations, covering the entire world, with much practical information, publications, references, etc.

► **THE CARNIVOROUS PLANTS** by F. E. Lloyd.—Since the appearance of CHARLES DARWIN'S "Insectivorous Plants" in 1875 no comprehensive treatise on these biologically exceedingly interesting plants has appeared. The gradual advance of our knowledge has been summarized from time to time by DRUDE, PFEFFER, ED. MORREN, HOOKER, GOEBEL and LLOYD, but a fully documented treatment was greatly needed. The illustrations are nearly all original and include numerous halftone plates, enabling the reader to visualize the forms discussed, and a large number of line drawings amplifying the text.—*A New Series of Pl. Sci. Bks.*, Vol. 9 (1942); Sup. roy. oct., buckram, 352 pp., several hundred illustrations.....\$6.00

Contents: Introduction. Heliamphora. Sarracenia. Darlingtonia californica. Nepenthes. Cephalotus follicularis. Genlisea. Byblis. Droserophyllum luisitanicum. Pinguicula. Drosera. The carnivorous Fungi. Dionaea. Aldrovanda. Utricularia. Biobularia, and Polypompholyx. Indices.

It is so clearly and entertainingly written that anyone with a modicum of botanical knowledge can enjoy it and use it as a guide. Professor LLOYD'S drawings and photographs are very clear and helpful, and the 38 plates incorporate hundreds of them. Production is of the high standard we have learnt to expect from Chronica Botanica. Altogether, a distinguished performance for which thanks and congratulations are due to both author and publisher (STEPHENS in J. So. Am. Bot.).

It is, therefore, the more commendable and welcome that finally LLOYD has completed this comprehensive authoritative, and detailed study of the carnivorous plants. Any such study which traces a function or an activity through the diverse

plants possessing it is bound to have a significant influence on science, and this authoritative volume without doubt will prove to be an epoch-making one. Comprising in large part the author's own original work, yet with a masterly synthesis of all the pertinent work previously done by others, the book has a thoroughness and completeness that stamp it as outstanding. All possible aspects of the plants concerned—their taxonomy, anatomy, physiology, ecology, and relationship—are considered in detail, with authoritative knowledge derived from the writer's 13 years of enthusiastic devotion to this field, devotion that involved careful absorption of an extensive literature in several languages, and first hand study of living material on this continent, in Europe, and in more remote localities during two journeys—one to Africa, another to Africa and Australia—supplemented by extensive correspondence, by securing the cooperation of collectors and naturalists in favorable localities, and by periods of study at various botanic gardens and laboratories....the volume is a beautiful job of craftsmanship (QUART. Review of Biol.).

► **TREE GROWTH** by D. T. MacDougal (Carnegie Inst. of Washington).—A presentation of the results of physiological and ecological studies of growth of pines, spruces, firs, larches, redwoods, cypresses, oaks, ashes, willow, poplar and other trees, beginning with the contributions of R. HARTIG and H. VON MOHL, and including the extensive observations of the author during the last twenty years.—Inception of growth, duration of seasonal activity of the cambium, correlation of growth in roots, trunks and buds, and relation of area of leaf-surface to volume of wood formed, receive comprehensive treatment.—*A New Series of Pl. Sci. Bks.*, Vol. 1 (1938); Roy. oct., 240 pp., 20 illustrations; out of print. Some time in the future we hope to publish a revised ed. or to include a treatment of the essentials of tree growth in a book on tree physiology. A few copies may still become available when we can again get in touch with our continental agents.

► **EXPERIMENTELLE CYTOLOGIE** von Hans H. Pfeiffer (Bremen).—The first comprehensive review by an internationally known and appreciated authority.—*A New Series of Pl. Sci. Bks.*, Vol. 4 (1940); Roy. oct., 243 pp., 28 illustr.; out of print. A few copies may again become available as soon as we will be able to get in touch with our agents in the Netherlands. A second revised and enlarged edition will be published some years after the war.

Experimental cytology is one of the most flourishing fields of research in present-day biology. The birth of the new sciences biophysics and biochemistry, the introduction of tissue culture, the inauguration of the periodical *Protoplasma*, and the appearance of several volumes on the physics and chemistry of protoplasm, all are indications of the great activity in this new field of scientific endeavor. To this new field, Dr. Pfeiffer has contributed his book on Experimental Cytology. There are twenty chapters, the subjects of which range from the structure of protoplasm, the permeability, vital staining, electrophysiology and the experimental control of development. The author's own research and world-wide relations give him the background necessary for a presentation of a discussion on cytology and genetics.

► **A LIFE OF TRAVELS** by C. S. Rafinesque (1836).—A complete and verbatim reprint of the extremely rare autobiography (1836) of this famous and eccentric naturalist.—*Chronica Botanica*, Vol. 8, No. 2 (1944); Sup. roy. oct., 72 pp., 5 portraits.....\$2.50

Contents: Life and Travels till the first departure for America. Travels in North America during three years. Ten years' residence and travels in Sicily. My shipwreck and travels till 1819. Seven years' residence and travels in Kentucky. Travels from 1825 to 1830, in Virginia, Ohio, New York, etc. Travels and researches 1831/33. The sources of the R. Delaware and Susquehanna. Conclusion. Travels and researches in 1834 and 1835, sources of the Schuylkill, central Alleghenies of Pennsylvania, Savings Banks, etc.

FITZPATRICK (1911) lists only 17 known copies in the libraries of the world. RAFINESQUE was born near Constantinople in

1785 and died in Philadelphia, Pa., in 1840. He is the author of more than 900 papers, chiefly appertaining to North America, covering such varied subjects as botany, zoology, medicine, history, archaeology, philology, banking, education, poetry, etc. Foreword by E. D. Mearns, and a critical index of personal names by F. W. Fawcett, the authors of several recent, critical papers on RAVENHURST.

► **A SHORT HISTORY OF THE PLANT SCIENCES** by H. S. Reed (U. of California).—A readable account of the growth of the plant sciences from early times to the present. The first 'History of Botany' written by an American and published in the U. S. A.—*A New Series of Pl. Sci. Bks., Vol. 7 (1942)*; Sup. roy. oct., buckram, 323 pp., 37 illustr....\$5.00

Contents: Introduction. Gardeners and Herbalists of Antiquity. The Nascent Period. The Retrogressive Period. The Renaissance Period. The Seventeenth Century. The Eighteenth Century. Gardens and Other Things. Plant Geography in the Nineteenth Century. Morphology. Cytology. The Water Economy of Plants. The Fixation of Carbon. The Assimilation of Nitrogen. The Fixation and Metabolism of Nitrogen. Plant Nutrition. Mineral Constituents in Metabolism. History of Mycology. Plant Pathology. Significant Names in the History of Botany.

REED'S "Short History" is more than a dry record of progress. Through the kind and appreciative eye of one of America's best-liked botanists the kaleidoscopic change in scenes and actors on the stage of botanical progress becomes a vivid adventure. This book will be enjoyed not only by professional botanists but also by students and others. . . . This book is thoroughly original, in scope and treatment as well as in illustrations. We do not find the traditional portraits of the paragons of science which often are of questionable authenticity and usually are entirely non-committal as to the character of the subject. Instead, original illustrations of significant experiments, laboratories or publications are depicted, with delightful originality. One of the special values of the book is the adequate, though not undue, stress laid on the contributions of American scientists. The reviewer was surprised to find how seldom he disagreed with the author, which can only be attributed to the care with which Dr. REED has considered each contribution and the sympathy with which he has treated each contributor. It is easier to criticize mistakes than to appreciate positive advances, which become incorporated in our general body of knowledge and which can be recognized as advances only after careful consideration (WENT in SCIENCE).

► **ESQUISSE DE MES VOYAGES AU BRÉSIL ET PARAGUAY, CONSIDÉRÉS PRINCIPALEMENT SOUS LE RAPPORT DE LA BOTANIQUE** par Auguste de Saint-Hilaire, with a biographical sketch by Anna E. Jenkins.—*Chronica Botanica, Vol. 9, No. 2*; Sup. roy. oct., ca. 80 pp., illustrated, in press, ready winter 1945.....\$2.50

This extensive travel account, reprinted from SAINT-HILAIRE'S *Histoire des Plantes les plus remarquables du Brésil et du Paraguay*, is being reprinted primarily at the request of a number of S. American botanists. Though in the first place of interest to botanists (the author gives an accurate description of his route) it contains much of a general biological, geographical and historical interest.

► **PLANTS AND VITAMINS** by W. H. Schopfer (Univ. of Berne), authorized translation from the author's unpublished French-Swiss manuscript by Norbert L. Noecker (U. of Notre Dame). Foreword by W. J. Robbins.—A critical review of the vitamin problem, written from the viewpoint of general physiology, transecting the various fields of biology; microbiology, plant and animal physiology, biochemistry, morphology, cytology, genetics, medicine, plant pathology, horticulture, and agriculture. The practical applications of vitamin research are given special consideration. The theoretical aspects are also treated and should be of interest to students and teachers of general biology.—*A New Series of Pl. Sci. Bks., Vol. 11 (1943)*; Sup. roy. oct., buckram, 300 pp., 20 illustr.....\$4.75

Contents: The Plant Cell and its Capacity for Synthesis. The experimental Study of Growth Factors and the Selection of Test Plants. Classification, Terminology, and Definition of Active Substances. The principal Vitamins synthesized by Plants. Their Action on Plants synthesizing them. The Biosynthesis of Vitamins. Thiamin. Yeast and Bios. Nicotinic Acid, its Amide, and other Analogues. Staphylococcus aureus. Riboflavin, Pyridoxine, and their Analogues. The Lactic Bacteria. The nitrogen fixing Bacteria. The Hemophilic Organisms and their Group of Growth Factors. Individual Factors: Ascorbic Acid, Cholesterol and Vitamin D, Fimelic Acid, the SH-Group. The Function of Growth Factors of Vitamin Nature. The Vitamins as Coenzymes. The Vitamins in relation with other active Substances. General Consideration concerning the Presence and the loss of the Capacity for Synthesis. Vitamins in Nature. Their Role in Agronomy and Horticulture. Vitamin Cycles. Growth Factors and Sexuality. Symbiosis, Parasitism, and Vitamins. Microorganisms as biological Test Objects for Vitamins.

It is that rare thing: a complete textbook. Apparently everything relevant has been included, and the matter is right up to date as far as it is possible for it to be. 'Plants and Vitamins' gives the conspectus of a new subject—the use of plants for vitamins. Ten years ago there was not one convincing example of the importance of a known and characterized vitamin for the growth of any plant or micro-organism, though possibilities had been suggested by BOTTOMLEY, MISS MCKEADON and others, whose interest lay chiefly in the effects of organic manures and soils. Our knowledge of the relation between plants and vitamins has come largely from the work of Dr. SCHOPFER, who since 1933 has been Professor of Botany in the University of Bern. The basic experiments on the thiamin requirements of the fungus *Phycomyces* are due to him; and in this book he presents the whole story. He has been ably aided by the translator (NICOL in SOILS and FERTILIZERS).

Few studies in biochemistry have aroused such popular interest as the remarkable advances made in recent years concerning the dependence of animals on small doses of those substances, produced mainly by plants, which we call the vitamins. It is natural that the marked heterogeneity for these substances in man has stimulated interest, largely in the vitamin aspects of animal nutrition; but it has always seemed anomalous that the importance of vitamins to the plant which makes them, realized only vaguely even by many botanists, has not had wider publication. This gap has now been filled in this remarkable book, and it is well that the first major review should come from the hands of an expert, and indeed one who may be said to be the founder of the modern science of plant vitaminology. His book is, as it must be, of the nature of a preliminary report on a subject now in the full tide of development; but it tells, in an orderly way, of all the important advances made in the ten years since SCHOPFER (1934) first showed the necessity for vitamins in the culture of *Phycomyces*, with sufficient bibliography to enable enthusiasts to find other sources of information. It is further very satisfactory that the author, though not hesitating to reproduce and discuss the structural formulae of the vitamins and to emphasize the vitally important, if purely chemical aspects of vitamin structure, does not fall into the trap of making the work biochemical. It is a book written by a plant physiologist for plant physiologists (PRESTON in NATURE).

► **PLANTS AND PLANT SCIENCE IN LATIN AMERICA**, edited by Frans Verdoorn.—A collection of over a hundred accounts of the vegetation and plant resources (with information on agriculture, forestry, phytopathology, etc.) of the countries of Central and South America. Discussions of the aims and future of the plant sciences in Latin America. Several maps. About one third of this material has previously been published in *CHRONICA BOTANICA* and is now again presented after careful revision. The larger part consists of original contributions, not published before. All articles are by outstanding international authorities.—*New Series of Pl. Sci. Bks., Vol. 16 (1944)*; Sup. roy. oct., buckram, ca. 400 pp., 70 illustr., in press....\$6.00

Special features are the plates, often reproduced from classical publications, and the extensive introductory chapters by FORBES (Problems of Tropical American Agriculture), JOHNSTON and SMITH (Vegetation Types), FORBES (Economic Botany), and PENNELL (History). There is also a special supplement by KRUC who reports on plant breeding in C. and S. America.

► **FOREST SOILS AND FOREST GROWTH** by S. A. Wilde (Univ. of Wisconsin).—The subject

matter of a course given for upper class and graduate students in forestry, soils, botany, game management, and landscape architecture, embracing a wide field of biology and earth sciences pertinent to soils and forests. Deals at length with the origin and genetical properties of forest soils, their physics, chemistry, and biology, relation to forest vegetation, and importance in silvicultural management.—*New Series of Pl. Sci. Bks., Vol. 17*; Sup. roy. oct., buckram, ca. 240 pp., illustrated, in press, ready autumn 1944.....\$4.75

Contents: Historical and introductory. Genesis of forest soils. Genetic soil groups of the world: Upland soils. Genetic soil groups of the world: Hydromorphic and embryonic soils. Forest cover: its biological structure and its relation to environment. Physical properties of forest soils. Chemical properties of forest soils. Organisms of forest soils. Forest humus. Soil-forest types. Forest soil survey. Soils and tree planting. Amelioration of forest soils. Thinning and selective logging in relation to soils. Productivity of forest soil and forest management. Establishment of forest nurseries and control of nursery watering. Use of commercial fertilizers and lime in forest nurseries. Use of composts, liquid fertilizers, and green manure crops in forest nurseries. Adjustment of nursery soil fertility. Control of parasitic organisms in soils of forest nurseries.

A fair balance is maintained between the theoretical foundations and the practical aspects of forest land utilization. All phases of silviculture, viz., nursery practice, tree planting, and selective logging are treated from an ecological standpoint. The bibliography of several hundred references is up-to-date and international in scope.

► **HAYFEVER PLANTS, THEIR APPEARANCE, DISTRIBUTION, TIME OF FLOWERING, AND THEIR ROLE IN HAYFEVER, WITH SPECIAL REFERENCE TO NORTH AMERICA** by Roger P. Wodehouse (Lederle Laboratories).—An authoritative botany of hayfever by the author of 'Pollen Grains'.—*New Series of Pl. Sci. Bks., Vol. 15 (1945)*; Sup. roy. oct., buckram, 245 pp., numerous illustrations and tables.....\$4.75

Contents: The Botany of Hayfever. The Hayfever Plants: Gymnosperms, Angiosperms, Monocotyledons, Dicotyledons. Regional Surveys. Glossary. Bibliography.

The first and larger part of the book is devoted to pollen and pollination and the part that pollen plays in hayfever, as well as the descriptions of all of the plants known to cause hayfever, showing where they grow, when they flower and the characteristics which make them hayfever plants. The second part of the book is geographical, dealing with hayfever by areas throughout the United States, Canada and Mexico. Numerous illustrations of plants and their pollen grains.

► **AN INTRODUCTION TO HISTORICAL PLANT GEOGRAPHY** by E. V. Wulff (Leningrad), authorized translation by Elisabeth Brissenden.

Foreword by Elmer D. Merrill.—An original and authoritative account of the general and theoretical problems of historical plant geography, based on the author's famous Russian handbook, revised and brought up-to-date. This American edition has been prepared at the request of botanists from many parts of the world, as there exists not a similar modern book in English, German or French.—*New Series of Pl. Sci. Bks., Vol. 10 (1943)*; Sup. roy. oct., 223 pp., 35 illustr.....\$4.75

The last few years have furnished to the phytogeographer such valuable new tools and so much fresh evidence, that a phase of expansion of the subject clearly lies ahead. Of this our botanical students are vaguely or not at all aware, and this first English text to reveal the new potentialities must therefore be valuable and welcome.—We can best convey the content of the book by the chapter headings: (1) historical plant geography; scope, relation to allied sciences, methods of investigation; (2) history of the science; (3) areas, their centres and boundaries; (4) the origin of areas; (5) types of areas; (6) parallelism in the geographical distribution of plants and animals and correlation between the distribution of parasites and that of their host plants; (7) artificial factors in the geographical distribution of plants; (8) natural factors in the geographical distribution of plants; (9) the migrations of species and floras and their causes; (10) historical causes for the present structure of areas and the composition of floras; (11) concept of floral elements (Gonwim in Nature).

In spite of the war, and that means much more in Russia than in America, it has been possible to arrange for Miss BRISSENDEN to work in close association with Dr. WULFF in Leningrad and then to publish the completed manuscript in this country. Once more science surmounts international boundaries and the catastrophes of war. As Dr. MERRILL states this volume "is a mine of logically and authoritatively discussed information on the subject." The book will be of special value to plant geographers, because it analyzes a large amount of continental, especially Russian, literature not otherwise readily available (MATIER in AMERICAN SCIENTIST).

► **MARINE MICROBIOLOGY** by Claude E. ZoBell (Scripps Inst. of Oceanography).—A monograph on hydrobacteriology with special reference to the distribution, characteristics, and activities of bacteria and allied microorganisms in oceans, seas, and lakes.—*New Series of Pl. Sci. Bks., Vol. 18*; Sup. roy. oct., buckram, ca. 250 pp., illustrated, in press, ready winter 1945.....\$4.75

Contents: Introduction. The marine environment. Collection and examination of samples at sea. Methods of enumerating marine bacteria. Factors influencing the distribution of bacteria in the sea. Microorganisms in bottom deposits. Activities of microorganisms in bottom deposits. Characteristics of marine bacteria. Aquatic yeasts and molds. Transformation of organic matter. The nitrogen cycle in the sea. Bacteria which transform sulfur compounds. The phosphorus cycle. Relation of marine bacteria to flora and fauna. Microorganisms in marine air. Sanitary aspects of marine microbiology. Economic importance of marine microorganisms. Microbiology of inland waters. Index to species of marine microorganisms. Bibliography.

ANNALES CRYPTOGRAMICI et PHYTOPATHOLOGICI

This new Serial consists of memoirs (each forming a separate volume) devoted to general and systematic cryptogamy and phytopathology. It continues *Annales Bryologici* of which we published 12 volumes and 4 suppl. vols. between 1927 and 1939. Vol. 1, GARRETT, Root Disease Fungi and Vol. 2, HORSFALL, Fungicides (cf. supra) are in press. About two volumes will be published every year at prices ranging from \$4.00 to \$5.00, net.

